

# 7th European Federation for Primatology Meeting

**30<sup>e</sup> Colloque de la Société Francophone de Primatologie  
Strasbourg, France, August 21–25, 2017**

Editors: Brice Lefaux, Mulhouse, Fanélie Wanert, Hélène Meunier, Strasbourg

## 1 Plenary Sessions

### The Extension of Evolutionary Biology through Culture

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A rich literature has increasingly documented the pervasiveness of cultural transmission in non-human primates, and these discoveries have multiple important implications. One that has received much attention is relatively narrowly anthropocentric, applying this new found knowledge of primate culture to understand the origins of the extraordinary scope of culture in our own species. Another, the focus of the present talk, instead looks outwards to more broadly evaluate the significance of what we have learned about animal culture for evolutionary biology at large. Primatology has often pioneered the study of animal cultures that this enterprise depends on, but it is equally important to recognise the breadth of cultural phenomena across the animal kingdom when addressing the wider questions about their role in evolution. In this talk, primatology remains as the core and foundation, but I additionally survey the picture of cultural phenomena revealed in recent decades of studies ranging over such groups as cetaceans, birds, fish and even insects. I consider three main implications of animal culture for evolutionary biology. First, culture replicates several core components of Darwinian evolutionary processes, potentially generating a new form of evolution in its own right. Second, this new form of evolution also has its own novel and distinctive characteristics, that reconfigure the way in which evolutionary processes work. Thirdly and finally, the two evolutionary systems, one based on genetic transmission and the other dependent on the “second inheritance system” of social learning, interact in forms of gene-culture evolution, with profound consequences for evolutionary biology.

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## Evolution of Grasping and Manipulation: From Behaviour towards the Interpretation of Fossils

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In primates, several selective pressures are thought to have led to the evolution of grasping and manipulative abilities including predation, locomotor mode, social context, food properties and tool use. In such a context, it is fascinating to try to analyze how parameters such as the variability of behaviours, morphologies, environments and diets interact, to understand the mechanisms underlying the evolution of these functions and finally try to infer hand use in fossil forms. An interdisciplinary approach allows us to address several issues: (1) which parameters are involved in the origins and evolution of grasping and manipulation among primates? (2) How do behavioural and morphological parameters interact? (3) How to infer hand use in fossil forms? We demonstrated that food properties affect manipulative strategies, especially mobile and/or embedded foods. It seems that strepsirrhines have simpler grasping strategies compared to catarrhines and that, among platyrrhines, capuchins have high finger individualization abilities. Among strepsirrhines, fur-carrying species (species who transport their babies in their fur and not in their mouth) exhibit significantly more frequent manual grasping of food items, and the mouse lemur can pull more than ten times its own body weight, probably in relation to its arboreal adaptation. Biomechanical studies showed that arboreal species tend to use more rotation of the upper limb joints than more terrestrial ones, who use more flexion-extension movements. Finally, humans show more complex in-hand movements than great apes, partly related to the shape of the trapeziometacarpal complex. Furthermore, behavioural and paleoanthropological data suggest that other species outside *Homo* are or were able to make tools. To conclude, I am convinced we need to develop integrative approaches and to study groups other than primates if we want to understand better the selection pressures involved in the evolution of manual grasping and manipulation.

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## Sexual Selection and the Differences between the Sexes in Mandrills (*Mandrillus sphinx*)

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Sexual selection is a major focus in evolutionary and behavioural ecology. It is also a popular research topic in primatology. I will use studies of mandrills (*Mandrillus sphinx*), a classic example of extravagant armaments and ornaments in animals, to exemplify how a long-term approach that integrates field observations with laboratory methods can contribute to on-going theoretical debates in the field of sexual selection. I will show how different reproductive priorities lead to very different life histories and divergent adaptations in males and females. Then, I will focus on male-male competition and female choice, followed by the less well-studied questions of female-female competition and male choice. These studies demonstrate how broadening traditional perspectives on sexual selection beyond the ostentatious results of intense sexual selection on males leads to an understanding of more subtle and cryptic forms of competition and choice in both sexes. This opens many productive avenues in the study of primate reproductive strategies, including the potential for studies of postcopulatory selection, female intrasexual competition, and male choice. These studies of mandrills provide comparison and, I hope, inspiration for studies of both other polygynandrous species and species with mating systems less traditionally associated with sexual selection.

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## Integrated Primate Conservation: The Role of European Zoos

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Integrated species conservation, also called One Plan Approach, is a new concept developing links between in situ and ex situ conservation. The zoo community focuses on long-term management of captive populations of threatened primates, without sometimes knowing the precise conservation needs of the species in the wild. On the other hand, field biologists and wildlife managers are more concerned with evaluating threats and protecting primates and their habitats, sometimes ignoring usable knowledge acquired in captivity. As 47% of primate species are considered as threatened in the Red List of IUCN (International Union for the Conservation of Nature) and threats to their habitats have never been so high worldwide, common efforts are needed to ensure their protection. Through the scope of ex situ programmes of primate conservation, we are looking at how the One Plan Approach could be implemented. Within the European association of Zoos, 80 primate breeding programmes managed at an EEP (European Endangered Species Programme) level are divided into 6 Taxon Advisory Groups (TAGs). Each TAG produces a Regional Collection Plan in order to prioritize the needs and intensity of management of the captive population with regard to their status in the wild. Three main issues are discussed: (1) How might the long-term viability of EEP primate populations influence the global future of the species in the wild? (2) Are the education, fundraising and research potentials of these EEP populations used efficiently by wildlife managers in protected areas? (3) Is a global management of wild and captive populations of the same species realistic? In situ analysis of conservation programmes and a viability assessment of the EEP population of *Eulemur flavifrons*, *Nomascus leucogenys*, *Cercopithecus roloway* and *Sapajus xanthosternos* allow us to determine different levels of integrated conservation implementation and to elaborate action plans at TAG level.

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## Facial Communication in Primates

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Facial expressions are ubiquitous among social primates, often appearing physically and functionally similar across species. Comparative studies are important, therefore, to understand the evolution of facial communication. The development of species-specific anatomically based coding systems (Facial Action Coding System: FACS) has greatly facilitated within-species and cross-species comparisons, and we now have modified FACS for use with various primates (chimpanzees, macaques, orangutans, hylobatids). These systems offer an objective, quantifiable and standardised method of studying facial expression, and remove the temptation to associate facial signals with emotion a priori. FACSs can be used to analyse the form and function of signals in detail, examining the impact of subtle changes in facial movement during a social interaction. FACSs can also be used to quantify expressivity in a species, and explore its relationship with socio-ecological variables in related species. Overall, our initial studies using such tools are helping to build an evolutionary framework for a better understanding of facial expression.

## 2 Oral Communications

### Oral Communications Cognition

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#### Evolutionary Origins of Money Categorization: An Experiment in Capuchin Monkeys (*Sapajus* spp.)

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Money is a cultural artefact which activates the same brain areas involved in reward processing. The ventral visual system in the human brain rapidly distinguishes between valid and invalid coins, regardless of familiarity. Since money is a very recent human invention, the ability of categorizing money may be traced back to non-human primates. Although non-human primates have not developed monetary systems, they can flexibly use tokens, i.e. inherently non-valuable exchangeable objects that arbitrarily stand for something else. Here we assessed whether token exchange is affected by token validity and familiarity in capuchin monkeys, which flexibly use tokens in several experimental contexts. Six capuchins were simultaneously presented with four types of items and required to exchange them in their preferred order within a 10-min time limit. They could choose among: (i) valid/familiar tokens: used in previous experiments, leading to a food reward, (ii) valid/unfamiliar tokens: introduced in the present study, leading to a food reward, (iii) invalid tokens: used in previous experiments, here losing their exchange value, and (iv) no-value items: introduced in the present study, without exchange value. For each subject, we recorded the order of exchange, the latency to exchange each item and the total number of exchanged items. Capuchins exchanged a similar number of valid/familiar and valid/unfamiliar tokens, and far fewer invalid tokens and no-value items. They exchanged first valid/familiar tokens, followed by valid/unfamiliar tokens, invalid tokens, and no-value items. Latency to exchange was higher for both invalid tokens and no-value items than for both types of valid tokens, although familiarity did not play a role. Thus, capuchins readily recognized token validity regardless of familiarity, as happens for humans with money. This suggests that money categorization is rooted in evolutionarily ancient abilities to process symbolic stimuli.

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Finding food is cognitively demanding for primates that generally live in unpredictable ecological conditions such as tropical forests. *What*, *where* and *when* an individual forages can impact fitness and, ultimately, species-level adaptations. To evaluate the relative weight of *what*, *where* and *when* on individual foraging decisions, we tested five Tonkean macaques in their social group in semi-free ranging conditions at the Primate Centre of Strasbourg University. We carried out four different successive foraging tasks, hereafter called seasons, and repeated them five times in the same order. In each season, we manipulated fruit availability by baiting a specific subset of boxes, fixed on trees and (un)lockable via a remote-control system, such that a season was characterised by a specific combination of fruit type, number and position of boxes. During the experiment, we recorded subjects' trajectories, the order of boxes visited. Task 1 investigated *where*, i.e. foraging patterns based on food location. Macaques readily optimized their route by choosing the shortest path in 16% of the trials where they visited all baited boxes ( $n = 64$ ), indicating that they did strategically plan their decisions. In the other cases, they mainly followed a "nearest neighbour" rule by choosing the closest box not yet visited, which implies an accurate representation of fruit availability. Preliminary analysis of tasks 2–4 (manipulating food density and quality) suggests a limited impact of *what* information on foraging decisions in this setting. The five repetitions of the four artificial seasons allowed us to investigate the influence of *when* information on their foraging pattern. Monkeys readily adjusted their foraging behaviour across seasons, further supporting the idea that foraging was based on accurate spatio-temporal mental maps of fruit availability. This study enhances our understanding of how primates integrate spatio-temporal food information to adjust their foraging strategies.

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Normal ageing is accompanied with a decline in several cognitive functions, including memory, attention and inhibition, related to prefrontal alterations. Because some of these cognitive declines are close to those observed in pathological ageing, a better understanding of normal ageing is essential to characterise pathological processes better. Because of their close phylogenetic proximity with humans, their complex cognitive abilities, and the development of prefrontal alterations through ageing that are similar to those of aged humans, macaques are appropriate models to study ageing effects on cognition. In this project, we tested (i) inhibition and attentional functions through 5-Choice Serial Reaction Time tasks, (ii) short-term memory through Delayed Matching to Sample tasks and (iii) working memory through Self Ordered Spatial Search

tasks. These three tasks were presented to a group of Tonkean macaques (*Macaca tonkeana*) using testing devices equipped with touchscreens and an automated identification system, to which they had free access from their enclosure at the Primate Centre of Strasbourg University. This group was composed of 30 Tonkean macaques aged from 2 to 21, living in semi-free-ranging conditions. This innovative approach is of key scientific interest: investigating memory, attentional and inhibitory functions in the same primate group composed of individuals of varied ages, directly in their living area. This enables the comparison of cognitive processes through ageing as well as their interactions with social aspects such as dominance hierarchy and social networks. Results show the more aged subjects show slower learning processes, attentional deficits and lower performances in short-term memory. These results enrich our knowledge about cognitive evolution through normal ageing, and better characterize macaque as an animal model for ageing processes.

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### **Psychological or Biological Approach to Personality? Method Comparison in Common Marmosets**

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Personality has been intensively studied in the past decades in various animal species, particularly in non-human primates. Two distinct approaches have been used to study animal personality: (i) psychological, that relies on scores obtained from questionnaires and (ii) biological, that relies on scores obtained from behavioural observations and/or behavioural tests. The convergent and discriminant validity of these approaches has been debated, but systematic research of the cross-method validity is scarce. In this study, we conducted behavioural observations and tests, and had trusted raters answer personality questionnaires about common marmosets (*Calithrix jacchus*) ( $n = 37$ ). We collected data independently in two different research laboratories (Vienna and Zurich) across two years (2011 and 2012), and analysed these data independently. We compared the component structures obtained by the two methods, and examined the correlations between the rating and behavioural constructs. Notably, all expected correlations and non-correlations were formulated a priori (we used Spearman rank-order correlations or Pearson product-moment correlations, depending on data distribution). The two methods yielded different trait structures, as was expected owing to the differing sets of variables in the questionnaire and behavioural data. Regarding convergent validity, some expected correlations were found, but none was found in both data sets, and several expected correlations were not found (e.g. explorative behaviour was not correlated with the construct Inquisitiveness). In contrast, discriminant validity was, with some exceptions, found for all constructs in both data sets. Our findings suggest that a re-evaluation of the questionnaires used in personality research is due. We will discuss how to improve the applicability of the questionnaires, and urge caution in choosing the most suitable methods to study personality in non-human primates.

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a partner, where the operator monkey was the only individual able to pull a tray to deliver food to both participants. Different distributions of food between the participants as well as the participants social relationships were studied. We observed that female squirrel monkeys were less willing to pull the tray altruistically to reward their partner when the latter was an out-group individual. Contrary to previous findings, our results suggest a sex-, context- and social-specific disadvantageous inequity aversion in squirrel monkeys.

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## Sex Differences in Immature Chimpanzee Play Communication

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In chimpanzees, as in humans, there are sex-specific differences in development that may be reflected in adult behaviour. These differences have been examined in sociality and tool-use, but relatively little is known about the development of sex-specific elements of adult chimpanzee communication. Play has been established as a context in which immature individuals can explore social behaviour. Here, we explore gestural communication employed in immature chimpanzee play, and compare and contrast this with gestural communication employed by adult chimpanzees. Using data from a longitudinal study of the Sonso chimpanzee community in the Budongo Forest Reserve, Uganda, we analysed 1,155 videos taken between 2007 and 2012 and coded 1,359 gestures produced during play by 25 immature individuals (14 females, 11 males; aged 1–12 years old). We recorded the choice of play partner in terms of identity, age, sex, and relationship (mother-infant, maternal-sibling, other), and described the gestural repertoire used to solicit, continue, change, and stop play by different age-sex groups. Within this data we investigated whether sex differences in immature play behaviour (partner choice and gesture use) reflect sex differences in adult social behaviour outside of play. We found sex and age differences in play partner choice: immature male chimpanzees requested play from a greater range of partners and from older partners, as compared with immature female chimpanzees. Moreover we found that the repertoire of gestures used to request play by immature male chimpanzees was more likely to incorporate those associated with sexual solicitation and display in adulthood than the repertoire of gestures used by immature female chimpanzees. Our results support the hypothesis that immature play may provide an appropriate environment for exploring sex-specific mature behaviour in chimpanzees.

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## Are There Teachers among Common Marmosets? And if There Are, Are They Sensitive to the Immatures' Skill Levels?

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Functional teaching in animals can be identified based on three broadly used criteria without the need to know about their intention to teach. Based on these criteria, teaching has been identified in a variety of taxa. It is not known, however, if animals also engage in intentional teaching, which is characteristic of human forms of teaching. During intentional teaching, teachers are sensitive to the naïves' skill deficits and adjust their behaviour accordingly. In this study, we first examined whether common marmosets exhibit teaching at the functional level. For this



purpose, we trained 24 adults until they were proficient in solving prey-extraction tasks, and subsequently observed their behaviour when solving these tasks in the absence or presence of immatures. We found that (i) adults changed their behaviour in the presence of immatures compared to when alone, (ii) adults incurred costs in investing energy in the extraction of a reward, and by sharing it with the immatures, and (iii) immatures learned the correct manipulation of the puzzle-box earlier than their twin siblings with individual learning. Thus, marmosets fulfilled the criteria for functional teaching. In addition, we investigated if adults were sensitive to the skill deficits of immatures to identify intentional teaching. For this part, we examined food sharing from adults to immatures, which is part of their cooperative breeding system, to see if the same adults shared more food items if they had previously observed that the immatures were unable to access the reward independently, compared to easy accessible rewards. Adults indeed preferentially shared food items that the immatures could not access independently, compared to easily accessible food items. Together, these results suggest that common marmosets engage in intentional teaching, which is of importance to understand the evolution of intentional teaching in human and non-human primates.

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## Literature Survey of Potential Cultural Variants in Japanese Macaques (*Macaca fuscata*)

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A huge amount of evidence has now accumulated for traditions in non-human animals, particularly non-human primates. Behaviours seen in free-ranging Japanese macaques were among the first potential traditions reported for any non-human animal, most notably “sweet potato washing” and “wheat placer mining” on Koshima Island, Japan. Numerous possible cultural variants have since been reported for this species, sometimes in Japanese only. Multiple long-term research sites have been subject to decades of detailed observation including: Arashiyama, Takasakyama, Koshima, Kinkazan and Yakushima Island. We reviewed the existing literature for behaviours reported as potential traditions. We aim to present a comprehensive synthesis of potential traditions in this species. We categorised potential traditions into food (foraging/processing behaviour or food choice) and non-food related (social/communicative, comfort/hygiene or other) behaviours. We further categorised each as directly related, indirectly related or unrelated to human influence, including provisioning. Prevalence was categorised, at the time of report, as customary, habitual or unknown within each site and named group. We identified a total of 37 potential behavioural traditions from the existing literature; 17 related, and 20 apparently unrelated to human influence. We could not determine the pattern of variation across all sites for each behaviour because cross-site comparisons were mostly limited to a few populations (with exceptions: stone handling, stone throwing, non-conceptive sexual behaviour and embracing), resulting in missing “data-points.” This species shows a high number of potential traditions but further research is needed to reveal occurrence of multiple potential traditions across the studied populations and whether this represents complex cultural variation. Delineating traditions in wild and free-ranging monkeys may help us to understand better the phylogenetic origins of human culture.

## Oral Communications Evolution

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### Primate Quadrupedalism and Developmental By-Products Point to the Origin of Bipedality

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In primates, infants commonly exhibit a more diverse positional repertoire than adults. The development thus constitutes a source of variation upon which selection may act. From this point of view, considering infancy opens new perspectives to address how (new) locomotor modes improved during primate evolution. In this respect, we assessed the relationship between two distinct modes during the development of olive baboons (*Papio anubis*): quadrupedalism and bipedalism, considered as the primary and the secondary locomotor modes, respectively. The focal sampling method enabled us to longitudinally record the locomotor behaviour of 6 infant baboons (from 5 to 22 months of age) at the CNRS Primatology Station (Rousset, France) where a large colony of baboons is housed. Using a video analysis software, we analyzed the temporal gait variables (duty factor, degree of regularity, etc.) and the behavioural parameters (frequency, mean duration, etc.) of quadrupedal and bipedal walking. Results show that the regularity of the interlimb coordination pattern, i.e. the relative timing between limb phases, improves in quadrupedalism and the proportion of quadrupedal behaviours increases with age. At the same period, while basic temporal aspects of the bipedal gaits do not change, infants improve their bipedal step regularity and the bout duration of spontaneous bipedal behaviours increases. During the baboon's early infancy, the ability to walk bipedally thus improves together with the development of interlimb coordination in quadrupedalism. It supports the hypotheses: (1) that a secondary locomotor mode, experienced during infancy as a by-product of locomotor development, may lead to evolutionary novelties during primate evolution, and (2) that the modular neural networks for quadrupedalism could also be employed for the elaboration of (occasional) bipedal walking. In this respect, a repertoire where the bipedal equilibrium became dominant could have (easily) originated from a quadrupedally oriented repertoire.

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### Ancient Admixture and Population History in *Pan* Species

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High-throughput sequencing development has been fuelling the field of population genetics and comparative genomics to move forward. Multiple genomes from different populations have played a valuable role in revealing current and historical population history. In humans, population admixture and ancestry in modern populations have been described in detail, suggesting how the peopling of different parts of the world has taken place, and a good picture of population history has been established through studies of archaic human populations such as Neanderthals and Denisovans. This has allowed the identification of signatures of bottlenecks and small effective population sizes over time in humans. Recently, we have presented the first evidence for admixture between the two *Pan* species, from bonobos to non-western chimpanzees. We further analyzed genomic segments inferred to be introgressed, and found that some of them appear to

have amino acid changes in genes relevant for reproduction, possibly suggesting adaptive introgression. We further study the same dataset to detect the genomic signatures of the demographic history in each population of the *Pan* clade, we find that deleterious mutations (assessed by scores such as SIFT and Grantham) are more effectively removed from the central chimpanzee population compared to other *Pan* populations, and do not reach fixation or high frequencies as expected from their higher historical effective population size. On the other hand, western chimpanzees, which used to have a small effective population size and went through bottlenecks, show an elevated level of deleterious load at homozygous loci. These observations agree well with predictions based on the demographic history, and add a valuable perspective to comparable findings in human populations.

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### **Hunting of Birds and Gathering of Eggs and Nestlings by Captive Cotton-Top Tamarins (*Saguinus oedipus*)**

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Hunting and meat eating have long been considered key behaviours in human evolution and it has been proposed that there is a basic primate predatory pattern from which hominin predatory behaviour may have evolved. Although hunting has been reported for several non-human primate species both in the wild and in captivity, such reports remain scarce. Even more rare are reports of egg and nestling gathering by primates. Here we report the first systematic data on bird hunting, and egg and nestling gathering by captive cotton-top tamarins (*Saguinus oedipus*). The monkeys exhibited specific behavioural patterns during the hunting and consumption of the birds: an initial bite on the bird's head, the emission of a food-related call during the consumption of the bird, and hand preference during the manipulation of the bird. Three different strategies to forage for birds and their products were distinguished: initiator, joiner and opportunist (individuals initiating searching episodes at a significantly greater frequency than expected, significantly lower frequency than expected and at an expected frequency, respectively). However, no strategy was found to be the most successful. The birds developed anti-predator strategies in response to the predation pressure exerted by the cotton-top tamarins. Although the cotton-top tamarins hunted the birds when they had the chance, the monkeys seemed to increase the possibility of a successful hunt by spending time every day monitoring the birds and their nests. Similar to reports on the hunting behaviour of other primates in captivity, the cotton-top tamarins in our study readily took advantage of the opportunity to obtain animal prey. We discuss the implications that our results have for the evolution of primate predatory behaviour.

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### **From Life History Traits to Social Parameters**

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Three kinds of data are considered in this study. Cranial morphologies and their modifications during growth are analyzed through a 3D geometric morphometric study of 1,400 hominoid crania. Life history traits in relation to growth are analyzed using a factorial correspondence

analysis. Social data record group sizes in the same hominoid species. The analysis of Procrustes residuals allows separation between species showing a rapid growth and species showing a slower growth. It appears that species showing a rapid growth are those which live in small groups, whereas species showing a slower growth are those living in large groups. Species with rapid growth can have the same growth between the sexes, no sexual dimorphism, and their social structure is monogamy, or they can have different growths, shorter in females and longer in males, sexual dimorphism, and their social structure is polygynous, in small groups. Species with slower growth can also have either heterogeneous growth, moderate sexual dimorphism and live in large fission-fusion social groups, or have more homogeneous growth between the sexes, weak sexual dimorphism and live in large social groups made up of several (more or less) monogamous social units. This study shows that growth speed added to sexual dimorphism may allow a more precise reconstruction of social structures. Estimating growth speed from crania in fossil hominoids would allow one to reconstruct their social structures and to work toward an understanding of social evolution through time in hominoids.

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### Heterogeneous Selection on Vomeronasal Receptors Over Time in Mouse Lemurs (*Microcebus spp.*)

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Olfactory communication is essential for nocturnal mammals and many species possess a functional vomeronasal organ (VNO) with a variable number of vomeronasal receptors (VRs) of two types (vomeronasal-1 receptors and vomeronasal-2 receptors). The small nocturnal mouse lemurs of Madagascar are thought to possess the largest number of VRs (~200) among all primates. The high diversity of VRs within this clade has been explained by their adaptive diversification and is most likely related to the fundamental relevance of olfactory communication and predator recognition in these primates. Chemosensory genes are often the target of positive selection, but little is known about the persistence of selection across different time scales. Therefore, we aimed to compare the selection regimes acting on VRs during their original diversification within the genome and during mouse lemur radiation with the selection regimes that may be still acting in natural populations of mouse lemurs on Madagascar. For this purpose, we first investigated signals of positive selection among 105 full length V1R loci in the grey mouse lemur and within seven V1R loci amplified across multiple mouse lemur species. To infer ongoing intraspecific selection regimes, we sequenced 17 VRs in sympatric populations of two species of mouse lemurs (*M. murinus* and *M. ravelobensis*) in northwestern Madagascar. Whereas the genomic analyses and the interspecific comparisons revealed strong signals of positive selection across large parts of the VR repertoire, the population samples, in contrast, suggest the effect of purifying selection, with one locus even showing evidence of functional loss in *M. ravelobensis*. Only a few loci in *M. ravelobensis* showed evidence of positive selection. The discordance of the two analyses may indicate that early beneficial mutations at VRs may have been fixed over a short period of time during mouse lemur evolution and that VR evolution may have been rather heterogeneous and episodic over time.

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## Miombo Woodland and the Origins of Bipedalism

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For several decades, bipedalism has been considered to be a key marker of human evolution and was suggested to have emerged in an open savannah environment despite the fact that Pliocene hominids (term restricted to humans and their forerunners) were known to be partly arboreal, partly terrestrial. In 2000, field discoveries suggested that human ancestors lived in Africa around 6–7 million years ago. *Orrorin tugenensis* from the Upper Miocene of the Tugen Hills (Kenya) is the only Miocene hominid species which preserves parts of the post-cranial skeleton which indicates a duality of locomotion. Whilst its climbing adaptation was different from that of the chimpanzee, its bipedalism was different from that of modern humans. But what kind of environment could have favoured such adaptations in a short-faced hominid? Savannah is a mixed environment with extensive grassy areas and wooded patches in tropical and sub-tropical zones with alternation of dry and wet seasons. Whereas most authors have focused their research on the emergence of grasses, the structure of the arboreal environment has been poorly researched. Here we suggest that miombo woodland would be an appropriate environment because it has a predominance of vertical supports (refuge to avoid predators) and trees are separated from each other: this morphology would be compatible with the locomotor anatomy of the early hominids (hand with opposable thumb and precision grasping abilities) elongated femur (advantageous for moving long distances; scattered food resources). It would also be consistent with the available data concerning Upper Miocene palaeoenvironments which suggest the occurrence of wooded grassland with patches of woodland. Miombo woodland is widespread in Africa south of the equator, currently ca 15% of the area of Africa, but it might have been more extensive in the past, reflecting differences in climate in the Upper Miocene.

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## Major Histocompatibility Complex Molecular Evolution in Western Chimpanzees (*Pan troglodytes verus*)

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Many species are threatened with extinction and their population size is decreasing greatly. A likely consequence is reduced genetic diversity which may have a dramatic effect on a population's survival. High diversity is crucial for MHC genes, which are involved in immunity, as it determines the disease and parasite resistance of individuals. Studies investigating the relative role of natural selection and genetic drift on MHC genes in populations of reduced size have returned contrasting results, either observing a reduced or a greater diversity than neutral markers. Based on a variety of evidence, including a low diversity in part of the MHC region, it has been suggested that chimpanzees have experienced an ancient selective sweep due to a viral epidemic most likely caused by an SIV-like retrovirus. A concomitant population bottleneck was inferred from whole genome data also. From collected published genotypic data, we estimated several statistics of genetic diversity in 4 cohorts of western chimpanzees and 51 to 89 human popula-

tions from 10 geographical regions at 7 MHC genes. Our analyses revealed a similar inter-locus diversity pattern in humans and chimpanzees, as well as an identical pattern of linkage disequilibrium. This suggests a highly conserved genomic region and evolutionary mechanisms in both species despite several million years of separate evolution. Based on a finer comparison of genetic diversity at the 7 loci between chimpanzees and humans, we also propose a tentative scenario for the molecular evolution of each MHC gene in the context of the past demographic history of western chimpanzees. Namely, we suggest that following a likely reduction of diversity, several MHC genes would have recovered allelic and/or nucleotide diversity while others would have retained a low diversity. The observed recovery of diversity at some genes after a bottleneck is thus quite hopeful for endangered species with very low population sizes if, of course, the population sizes increase again.

## Oral Communications Human and Social Sciences

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### On the Rocks: Using Discourse Analysis to Examine Relationships between Barbary Macaques (*Macaca sylvanus*) and People on Gibraltar

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The goal of this study is to understand people's perceptions of the introduced Barbary macaques on Gibraltar and find potential solutions for human-macaque conflict. We use discourse analysis as a qualitative method of examining the attitudes underpinning the tumultuous (or ambivalent) relationships between resident people and macaques on Gibraltar. We apply it to the complaints and comments made in the public Facebook group "Monkey Sightings," which has over 1,000 members. Results indicate that Barbary macaques on Gibraltar occupy a niche in which they are viewed both with pride and a sense of ownership (often referred to as 'our monkeys'), as well as with mistrust and fear. Many residents complain that the monkeys do not stay in "their" place, instead straying into urban areas and acting as invaders. They also attribute damage caused by the macaques to wilful enjoyment, and refer to them using a vocabulary that connotes predation, as they are said to form "packs" rather than "groups" or "troupes." Residents also express anger at the Ministry of Environment which is perceived as being in charge of the macaques, and demand that more measures be undertaken in order to keep them away from urban areas. These preliminary findings show that the relationship between people and Barbary macaques on Gibraltar is complex and volatile. They point to implications for Gibraltar's authorities as well as for the macaques and the people affected by their presence in urban areas. Sensitisation programmes and awareness-raising efforts exist, but greater collaboration with residents is needed to prevent the development of more intense human-macaque conflict.

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## Human Cumulative Culture Evolution: New Lights on Overimitation from a Developmental and Cross-Cultural Study

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Cumulative culture has played a central role in our evolutionary success and may rely, in humans, on innovation and imitation. Recently, attention has focused on how these features develop through childhood and compare to other animals, allowing for evolutionary and comparative perspectives. Developmental studies have shown that young children are skillful at acquiring tool-using skills by copying actions performed by others to succeed in a task, and contrary to great apes, they “overimitate,” replicating both relevant and irrelevant actions. Strikingly, young children are poor at manufacturing new tools when solving problems. However, among other limitations, studies on overimitation have almost exclusively used a puzzle box on which the model performs both relevant and irrelevant actions with the same tool before retrieving a reward. Thus, high rates of overimitation may arise from paying too much attention to this single object, increasing its normative aspect. Therefore, it was unclear whether children would overimitate in a more realistic context in which several tools are involved. Here, we presented 5- to 12-year-old French ( $n = 102$ ) and Serbian ( $n = 106$ ) children with a *Hook task* in which children had to recover a reward from a jar using a pipe cleaner as relevant tool material. In both cultures, few children under ten years of age manufactured a hook to retrieve the reward; however, from 5 years of age onwards, the majority succeeded after seeing an adult demonstrating how to make a hook without explicitly modelling its final goal. Additionally, a third of the children replicated the irrelevant action performed with a second object. Our results show that children’s difficulty with innovation and capacity for flexible overimitation do not depend on socio-economic background. Finally, a surprising sex effect appeared during overimitation, shedding new lights on our understanding of how human tool culture evolved.

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## Good Gibbons and Evil Macaques: A Historical Review of the Cognitive Style of Non-Human Primates in Traditional Chinese Culture

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For several thousand years the ancient Chinese have accumulated an extensive knowledge, in the form of written literature and folklore, on the non-human primates widely distributed in China. Several studies have focused on primates in Chinese traditional cultures, including novels, legends, painting, poems, and monkey shows. However, previous studies mainly focused on specific subjects, either the gibbon or the “Sun Wukong,” and did not mention differences between the two animals in Chinese traditional understanding, or when the ancient Chinese noticed the difference between apes and macaques. We used the methods of critical text analysis and discourse analysis in order to show when and how ancient Chinese started distinguishing gibbons from macaques. We divided the period of historical research into four main stages: Pre-Shang to



Shang Dynasty (before 1046 B.C.), Zhou to Han Dynasty (1046 B.C.–220 A.D.), Six Dynasties to Song Dynasty (220–1279 A.D.) and Yuan to Qing Dynasties (1279–1840 A.D.). We found that China's traditional cognition of gibbons and macaques emphasized the morphology of animals, their organoleptic performances and even whether their behaviours were "moral" or not. People judged animals by ethical standards and emphasized the creature's usefulness to humans, but ignored the physical characteristics of the animals. Therefore, Chinese ancients did not care about biological distinctions between gibbons and macaques, but left many expressions on "good gibbons and evil macaques" in folklore, poems, local records, etc. This kind of cognitive style actually embodies a feature of Chinese traditional culture. This study is expected to fill a research gap in our knowledge on primate cultures and to present some original views on Chinese traditional knowledge of primates.

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### **The People's Voice: The Missing Component of Javan Gibbon Conservation**

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Knowing how people perceive and relate to the environment is invaluable to conservation efforts. The mechanisms that drive conservation initiatives are social in nature, and it must be acknowledged that conservation is as much about people as about the environment and non-human species. The goal of my research was to explore how local communities living on the border of Gunung-Gede Pangrango National Park in West Java, Indonesia, perceive the natural environment and the wildlife with which they share the forest. More specifically, the goal was to determine the depth of their knowledge about Javan gibbons (*Hylobates moloch*) and the threats they face in the wild, and ultimately, how they understand the concept of "endangered species." I conducted face to face, semi-structured interviews with over 100 people during the months of June through August, 2016. Interviews revealed an unexpected narrative. Local people lack sufficient knowledge and information with regards to the forest and its inhabitants. Responses varied between how important people thought protecting the forest was, and how crucial the need to expand agriculture is for their personal livelihoods. Ultimately, the concept of "endangered species" is understood differently across cultures. In addition, there was an overwhelming response from the communities of not feeling "included" in conservation activities within villages, as well as in the national park. This study was the first step to examining how to initiate more inclusive conservation programmes that are not limited to providing economic welfare to local people. Support from local governments and communities is crucial to ensure the success of conservation programmes for Javan gibbons in West Java.

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### **Why International Agreements Fail to Protect Great Apes – Lessons from GRASP**

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Many international agreements deal with great ape conservation. One of them, the Great Ape Survival Partnership (GRASP), specifically focuses on this issue. Despite these agreements, all great apes are listed as "Endangered" or "Critically Endangered" on the IUCN Red List of

Threatened Species. This research seeks to understand this contradiction by focussing on GRASP. It assesses who is benefiting from GRASP, considering GRASP as an institution where each stakeholder uses its resources (e.g. expertise, media, rules, knowledge) so that the institution works to its benefits. The data are gathered from semi-structured interviews and Internet-based researches between 2000 and 2016. The study found that GRASP stems from the Ape Alliance, a British-based non-governmental advocacy coalition to protect great apes, and from the United Nations Environmental Programme (UNEP). In the name of meeting the general public's concerns over the fate of the apes, Ape Alliance and UNEP built a partnership around the paradigm of "radical conservation" that seeks to protect each individual and all habitats. They maintained control of the agreement and became the main beneficiaries through four interconnected additional loops: interpersonal relationships among international primatologists, financial flows, international scientific networks, and media exposure. They exerted asymmetrical power over actors who did not belong to these loops, in particular those from areas where great apes live (governmental institutions, firms, communities, or scientists). After 2012, the "ecosystem service management" paradigm emerged worldwide. Far from changing these relationships of power, those same dominating actors appeared in this new field and maintained their political positions. On the pretext of scientific expertise and standardization at the heart of the managerial logic of this new paradigm, socio-ecological contexts were omitted and local people were once again excluded from decision-making processes. In summary, GRASP has largely failed to achieve a tangible impact and to reduce threats on great apes because of its inability to address power asymmetries, to grasp socio-ecological contexts and to strengthen local stakeholders: all of these matter for long-term ape conservation.

## Oral Communications Conservation

### Assessment of Chimpanzee Nest Detectability Using UAV-Derived Aerial Imagery

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As with other great ape species, chimpanzee numbers have declined during the past decades. Proper conservation of the remaining chimpanzees requires detailed data on their abundance. Although it is estimated that in Tanzania there are 2,000–2,500 chimpanzees (*Pan troglodytes schweinfurthii*), more than 75% of those live at low densities on land outside national parks and little is known about their distribution, density, behaviour or ecology. Given the sheer scale of chimpanzee distribution across western Tanzania (>20,000 km<sup>2</sup>), we need new methods that are time and cost efficient while providing precise and accurate data across large spatial scales. Scientists have recently demonstrated the usefulness of Unmanned Aerial Vehicles (UAVs) to identify wildlife presence, including apes. Whilst identification of apes themselves is unlikely given their elusiveness, we investigated the potential of UAVs to detect chimpanzee nests in Issa valley, western Tanzania. Between 2015 and 2016, in both wet and dry seasons, we tested and compared the capabilities of two fixed-wing UAVs. Twenty-two survey plots (50 × 500 m) were surveyed in gallery forests and miombo woodlands to record nests from the ground, versus from the air. We

performed mixed effects logistic regression models to evaluate the influence of nest height, nest age, canopy openness, tree species and habitat on nest detectability. An average of 10% of the nests found on the ground were detected from the air with lower detection in the wet season, when the canopy cover is higher. We discuss the potential but also the limitations of this innovating technology to determine chimpanzee distribution and density. Combining traditional and more novel, technological methods of surveying allows more accurate collection of data on animal distribution and habitat connectivity, which has important implications for chimpanzee conservation in an increasingly anthropogenically disturbed landscape.

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## Increased Female-Female Competition in Wild Bornean Orangutans following Forest Fires

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Forest fires in tropical forest areas may have major consequences for animals. During 2015, forest fires devastated large areas in Kalimantan (Borneo), including orangutan habitat: 80 ha of the Tuanan research area (Mawas Conservation Area, Central Kalimantan) burnt down, reducing the size of several female orangutans' home ranges. Moreover, heavy smoke covered the canopy for three months. As a consequence, forest productivity was reduced, leading to a prolonged period of lower fruit availability during all of 2016. The resident female orangutans survived the unusually long food scarcity period by relying on fallback foods and switching to an energy-saving mode. In this study, we examined the combined effect of the low fruit availability and the reduced home ranges on the females' social interactions. Fourteen habituated adult female Bornean orangutans (*Pongo pygmaeus wurmbii*) were followed for a total of 487 full-day follows spread among 2012 and 2013, years considered as normal in term of fruit availability and home range size, and 2016, the post-fire year. Behavioural data were collected using the focal animal sampling method, with instantaneous data recorded every two minutes. We compared the time spent in female-female association, the location and the nature of the encounters between previous years and the post-fire year. We found that females spent less time in association with related females in the post-fire year. However, when females were in association, agonistic interactions were more frequent among both unrelated and related females, occurring mostly in the crowded parts of Tuanan. This pattern indicates increased female-female competition, via active avoidance, intolerance of proximity and aggressive chasing, over access to food resources but also over space. These findings draw attention to the costs of future habitat degradation on a wild population, and allow us to anticipate the consequences of reintroduction plans that may not consider the stress on resident females caused by the arrival of unknown females.

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## Anthropogenic Disturbance and Conservation Challenges in Tonkin Snub-Nosed Monkeys in Tung Vai and Khau Ca Forests

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The Tonkin snub-nosed monkey (*Rhinopithecus avunculus*; TSNM), is one of Asia's rarest primates and a unique example of a Lazarus species. Despite conservation attempts, anthropogenic disturbances such as agriculture and hunting have left fewer than 200 individuals in rem-

nant karst forests of north Vietnam. To investigate habitat status, anthropogenic threats, habitat use and home range of the two largest remaining populations, I surveyed Khau Ca and Tung Vai forests from mid 2016 to early 2017 to collect home range and daily range data. I used QGIS software and LANDSAT 8 imagery to compare disturbance and analyse land use at the two sites, and to calculate home ranges with seasonal variation with verification using 200 and 100 ground truth GPS points in the Tung Vai forest and Khau Ca forest, respectively. I calculated TSNM occurrence rates by collating direct observation and survey effort GPS data with a 24-month dataset collected by my research assistants. Preliminary analyses reveal sprawling agricultural processes as the dominant threat to TSNM in the Tung Vai forest where sub-canopy cardamom is grown, while few anthropogenic threats are apparent in Khau Ca. Log poaching is an evident threat at both sites, but a more extensive one in Tung Vai. Population survey results indicate a 48% population decrease at the Tung Vai forest over the 24-month period, which may be the result of hunting, poor habitat connectivity or erroneous survey results. The population at Khau Ca appears stable or potentially increasing with only one instance of log poaching recorded under anthropogenic disturbances. The results of this study highlight the concerning plight of TSNM, especially at Tung Vai forest, which may leave Khau Ca as the only viable population. To date, a strict protected area approach with patrolling staff appears to be the only effective solution. For this reason, I recommend that in conservation action plans priority be given to corridor connectivity to a nearby protected area to allow the potential expansion of the population at Khau Ca. I also recommend monitoring TSNM daily ranges, to further understand the ecology of this species and its habitat requirements.

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## A Community-Led Reforestation Programme in an Agroforest Environment

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As human populations and, thus, global deforestation rates continue to rise, conservationists are forced to re-examine approaches needed to maintain viable habitat. More and more threatened primate taxa are found in disturbed habitats, which are often the result of increased human activity. Therefore, our attention as conservationists must turn to working towards helping humans understand the benefits and complexities of living alongside primates and other taxa. In this study, carried out in Garut Regency, West Java, Indonesia, we examined the efficacy of a reforestation programme within an agroforest environment that is home to a substantial population of Critically Endangered Javan slow lorises (*Nycticebus javanicus*). The programme was designed to work with the local human population to provide solutions that would benefit wildlife and humans alike. Constant feedback was provided about the project to the community via biannual community festivals, monthly newsletters, annual calendars and a weekly Nature Club for children. Beginning in January 2015, we carried out extensive pre-project surveys of 96 local farmers to determine their priorities and needs. We then paired this information with long-term ecological data on the populations of *N. javanicus*, which have been collected at our field site continuously since 2011, to create a reforestation programme. This programme focused on three key tree genera vital for both farmers, in terms of soil stability and fuel wood, and slow lorises, in terms of canopy continuity and food – *Melaleuca*, *Calliandra*, and *Acacia*. We carried out the first round of planting in July 2016 and over the next 9 months we monitored 153 trees of three species. Early benefits after 1 year include increased soil support by the roots of the growing trees and increased awareness of slow loris ecology among the local population. We describe the next stages, including monitoring of change of slow loris' home ranges, and a planned honey production project using the flowers of one of the key planted species.

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## Identification of Animal Interactions with *Nauclea orientalis* along the Kinabatangan River, Sabah (Malaysia): Highlighting the Proboscis Monkey's (*Nasalis larvatus*) Role in Seed Dispersal

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Efficient conservation planning requires understanding plant-animal interactions; endozoochory for instance plays an important role in forest regeneration. Being mainly folivorous, the endangered proboscis monkey (*Nasalis larvatus*) has never been considered as a seed disperser. However, in previous studies intact seeds were found in their faeces. This study therefore aims to assess the role of the proboscis monkey in seed dispersal. It was conducted from November 2016 to April 2017 along the Kinabatangan River, in the Lower Kinabatangan Wildlife Sanctuary, Sabah. Preliminary results showed that approximately 60% of monkeys' faeces contained intact seeds; most of which were from the genus *Nauclea*, and that *Nauclea* seeds collected from faeces have a higher germination rate than seeds collected from fruits. Therefore, the focus of this study was the species *Nauclea orientalis*. Seed dispersal quantity and quality were examined. Other animal species feeding on *N. orientalis* fruits and potentially dispersing its seeds were also investigated. The research consisted of 57 sessions of boat-based behavioural observations of groups of *N. larvatus* (instantaneous scan sampling), faecal collection and germination tests as well as monitoring a river transect through boat-based surveys and camera trapping. Two Cercopithecidae, one Hominidae, one Suidae and one Tragulidae species were recorded feeding on *N. orientalis* fruits. Intact *Nauclea* seeds were also found in the faeces of four Cercopithecidae, one Hylobatidae, one Hominidae and one Viverridae species. Further analyses are being performed to highlight these species' respective importance in *N. orientalis* seed dispersal. In conclusion, since effective conservation of *N. larvatus* requires reforesting critical habitats and linking forest fragments, this study is meant to provide useful information for conservation planning and reforestation programmes.

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## Implementation and Evaluation of Two Education Tools (Movie Screening and Participatory Theatre) about the Critically Endangered Crested Macaque (*Macaca nigra*) among the Local Population in North Sulawesi, Indonesia

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Among the 7 macaque species of Sulawesi Island (Indonesia), the crested macaque (*Macaca nigra*), endemic to North Sulawesi, is Critically Endangered. In the past 3 generations, the crested macaque population has been reduced by more than 80% due to habitat loss and hunting pressure. The aims of this study were to implement two conservation education tools (movie screen-

ing and participatory theatre) among the local population of North Sulawesi, to enhance the conservation of crested macaques and assess the evolution of conservation knowledge before and directly after the conservation activities (lasting about 2 h) with a free-listing exercise. Seven events (with about 100 people attending each event) were held between June and July 2016 in villages and schools surrounding Tangkoko-Duasudara Nature Reserve. A total of 42 solutions to problems presented in the participatory theatre were obtained, mainly from men (40%) and pupils (26%), with fewer from women, teachers and officials. The majority of the solutions were pro-conservation statements. In total, 422 people participated in the free-listing activity before the conservation activities and 263 people after them. Data were analysed using SPSS 23 and Nvivo 10, and classified into 3 main categories: conservation knowledge, emotion or missing data. Different analyses, including inferential statistics, were used to show that knowledge of the conservation of crested macaques changed throughout the conservation activities (movie and participatory theatre). Participatory theatre could be considered as a preliminary way to explore issues pointed out during conservation activities and be used as an education tool to reinforce conservation messages, as many respected people, such as officials and teachers, spoke out for crested macaque conservation. The free-listing technique, as an assessment method for conservation activities, can quickly determine if conservation messages have been understood and adopted among participants. Therefore, the free-listing technique could be a quick, easy and interactive way to assess conservation activities for NGOs such as Tangkoko Conservation Education (TCE), which hosted the study.

## Oral Communications

### Social Behaviour

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#### Infrared Thermography as a Measure of Emotion in Barbary Macaques

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The study of emotions during naturally occurring social interactions has been hampered by the lack of feasible, non-invasive measures. A recent advance in emotion measurement is the use of infrared thermography, which, by measuring reflected radiation, can be used to quantify skin temperature. Changes in facial skin temperature have been associated with arousal and emotional valence in humans and captive non-human primates. Previous studies focused on emotions of negative valence and in highly standardized settings. Here we tested whether nasal temperature changes reflect emotional states in male Barbary macaques (*Macaca sylvanus*) during naturally occurring interactions of both positive (grooming) and negative (conflicts) valence. We predicted (i) a decrease (from baseline) in nasal temperature following conflicts, (ii) an increase following grooming, with (iii) the strength of the increase to be positively related to the strength of the affiliative relationship between the two grooming partners. Data were collected over a 3month period on 10 adult males from a large social group of Barbary macaques at Affenberg Salem, Germany, using event sampling on social interactions for thermography ( $n = 38$  conflicts;  $n = 28$  grooming events) and focal animal observations of social interactions for affiliative relationships strength (measured as dyadic composite sociality index). As predicted, nasal temperature decreased significantly from baseline following conflicts and significantly increased following grooming which had not been shown before. Contrary to our prediction, the stronger the affiliative relationship between the grooming partners, the smaller the increase in thermal change was.



Overall, this study adds to others highlighting the feasibility of infrared thermography as a non-invasive tool to investigate emotional states in non-human primates in non-standardized social interactions, highlighting its potential for research on primates in the wild.

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## Early Maternal Loss Affects Social Grooming Similarly in Wild-Caught and Captive-Born Male Chimpanzees

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Early maternal loss may influence later social functioning in human and non-human primates. Previously, we found social grooming to be more strongly affected in chimpanzees that were maternally and socially deprived in their early infancy (ED) compared to later deprived (LD) and non-deprived ones. In these studies, all deprived chimpanzees were captured in the wild. In addition to the loss of the mother, these wild-caught individuals also witnessed the killing of their mother and experienced a radical change in living conditions. Therefore, we expected wild-caught EDs to be more strongly affected in their social grooming activity than captive-born EDs who were rejected by their mothers. In the present study, we evaluated the social grooming networks of two all-male groups. One group, housed at the primate house in Gaenserndorf, Austria, consisted of 7 ex-laboratory individuals (6 wild-caught EDs and 1 LD) and was studied during the first year of group life. The second group, housed at the Kumamoto Sanctuary in Japan, consisted of 15 mainly ex-laboratory individuals (6 wild-caught EDs, 6 captive-born EDs, and 3 LDs) and had been stable for two years, though individual males had been socially housed for up to 20 years. We compared two different network measures reflecting the individual grooming activity and the evenness in the distribution of grooming among group members between wild-caught ( $n = 12$ ) and captive-born ED males ( $n = 6$ ). Contrary to our expectation, we found no difference between wild-caught and captive-born EDs, neither in terms of their grooming activity nor in their distribution of grooming among group mates. Moreover, there was no association between grooming network measures and years spent socially housed. Even though we cannot draw a clear causal link due to the retrospective nature of this and previous studies, our findings show that early maternal loss affects not only wild-caught but also captive-born chimpanzees' social grooming competence in the long-term.

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## From Primate Alliances to Elites or Classes in Human Societies

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Primate males form within-group coalitions and alliances in a variety of constellations whenever groups contain enough males to make them possible. However, none of the detailed field studies reports the presence of systematic alliances by the top-ranking males (an "elite"), apart from temporary all-down alliances to maintain a previously successful rank-changing (rev-



olutionary) alliance against individually stronger individuals. Similarly, no study of mobile or nomadic human foragers ever mentions the presence of such a dominant class or elite. Yet, among human food producers and to some extent sedentary foragers, we commonly see such elites. Here we ask whether we can understand this development as an example of a coalitionary strategy. Previously, we developed models of adaptive coalition formation among primate males to predict patterns in real-world primate groups. These models have shown a good enough fit with observed patterns in various species to warrant their use for this question. We found that elite formation is an inevitable outcome of male-male competition whenever dominants cannot only exclude others from resources (as in the case of non-human primates) but also exploit the fruits of others' labour (produce or property). The model thus provides a mechanistic basis for the phenomenon first noted by Marx and Engels, but also explains its distribution across social and subsistence systems within humans, in particular its absence among nomadic foragers.

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### **A Mathematical Model to Predict Hierarchical Rank in *Macaca mulatta* and *M. sylvanus***

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Several, sometimes conflicting, explanatory frameworks have been put forward to posit inter- and intraspecific variation in non-human primate social relationships, particularly with regards to the emergence of the hierarchical structure, like the “prior attributes hypothesis” (i.e. through individuals' intrinsic attributes), the “social dynamics hypothesis” (i.e. through processes of social behaviours), and the “ecological hypothesis” (i.e. through demographic and ecological factors). However, these hypotheses are considered non-mutually exclusive now. In the present study, we examine two individual attributes (age and matriline membership) for males and females in two macaque species (*Macaca mulatta* and *M. sylvanus*). The macaque genus is widely used as a biological model due to the numerous similarities (multimales, multifemales and multigenerational groups with matrilineal rank inheritance) and dissimilarities (dominance styles) across macaque species. We use a multiple hierarchical stepwise regression (MHSR) approach to build a multi-predictor model based on the “prior attributes hypothesis.” Our findings show that age and matriline membership explain most of the inter-individual variance in hierarchical rank for both sexes and both species (90.4–96.1% in female *M. mulatta*, 63.2–95.0% in male *M. mulatta*, 90.4–96.1% in female *M. sylvanus*, 63.2–95.0% in male *M. sylvanus*), suggesting not only the potential value of the prior attributes hypothesis, but also its likely weight in the explanation of the hierarchical structure. This analytical protocol permits the comparison of hierarchical structure between sex categories within a group, and could also be viewed as a tool for inter-species hierarchical comparison. This model also highlights the necessity to consider the prior attributes hypothesis in self-organised models based on social dynamics to gain a holistic perspective of how hierarchical structures emerge.

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The impact of kinship on primates has been extensively studied in cercopithecines. In fact, maternal kinship is considered one of the most influential factors structuring affiliative behaviour (spatial proximity, grooming, conflict intervention, etc.). In turn, affiliative and dominance behaviours define social structure in primates. Using the A-KinGDom agent-based model, we explored how maternal kinship affects the execution of affiliative interactions between individuals and modifies the social structure of the group depending on the social style displayed by each species. Our long-term aim is to develop a useful tool to predict changes in social structure in primate groups to plan management strategies for captive and semi-free-ranging groups. To assess the A-KinGDom model, we compared our simulation results with empirical results collected at the Primate Centre of Strasbourg University in a semi-free-ranging group of *Macaca tonkeana*. As expected, the simulation results suggested that maternal kinship increases the likelihood of observing an affiliative interaction in despotic societies but not in egalitarian societies. The simulation results also showed difference in social structure measurements depending on the social style (for example, despotic societies showed high values of unidirectionality of aggression and egalitarian societies showed high rate of affiliative behaviours due to post-conflict behaviours). We conclude that the simulation results agreed with the observed differences in social structure measurements in macaques societies depending on their social style. Additionally, as the A-KinGDom model can be adapted to different biological conditions (i.e. number of individuals, sex ratio, coefficient of relatedness between group members, initial dominance hierarchy, facility shape, etc.), it may be possible to use it to anticipate changes in social structure and facilitate the development of management strategies in captive and semi-free ranging groups.

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Female visual features are signals widely studied in primate sexual communication. In particular, sexual swellings, which seem to reflect intra-individual (timing of ovulation) and inter-individual (social and life history characteristics) variation, have received considerable attention. Relative to the study of exaggerated sexual swellings, fewer studies have investigated the role of face colour in sexual communication. In Japanese macaques (*Macaca fuscata*), the females express red colouration of the face, which undergoes seasonal changes through variation in circulating sexual steroids. Japanese macaques are seasonal breeders, and females must balance the costs of mating with other energetic costs linked to environmental factors, such as thermoregulation and food scarcity during winter. Here we aimed to determine if face colour (i.e. luminance

and redness) is informative about female reproductive status (cycling vs. pregnant), age, dominance rank, parity, and body weight. We also tested for links between face colour and infection with intestinal parasites, as measured by faecal egg counts and parasite species richness. Results indicate that female face luminance decreased from the pre-conceptive month to the pregnancy period, whereas face colour only varied between the 1st and 2nd months of gestation, with females becoming less red as pregnancy progressed. We found no evidence to suggest that female face colour is an indicator of any of the individual characteristic measures. Our results suggest that, among Japanese macaques, female face colour might not act as an indicator of individual quality, but rather as a signal of reproductive status. Females might not need to compete for mates through “quality signalling,” but may instead signal their pregnancy in order to decrease the overall costs of reproduction (i.e. male harassment, thermoregulation) and allocate their resources to foetal growth.

## Assessing a Method to Determine Spatial Proximity and Individual Centrality in a Group of Semi-Free-Ranging *Macaca tonkeana*

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Group spatial distribution is an important variable which can affect individuals' risk of predation, foraging success and social relationships. Individuals' spatial proximity and dominant individuals' centrality are crucial determinants of spatial distribution. There are few methods available for determining these elements in semi-free facilities where individuals can be located far away from each other. This research is a pilot study to determine individuals' spatial proximity and dominant individuals' centrality in a group of semi-free-ranging *Macaca tonkeana*, housed at the Primate Centre of Strasbourg University, applying Dolado and Beltran's (2011) method. We divided the facility (3,680 m<sup>2</sup>) into 11 areas and we defined different points in each area (i.e. 208 defined points). We recorded observations and determined the individuals' position every 30 s (i.e. assigning each individual to a defined point and area at each time). We calculated proximity between individuals with these data. For obtaining individuals' centrality, for each subject we calculated a unit vector towards every other subject. Each subject's centrality is the module of the sum of its unit vectors towards all the other subjects. Subjects with smaller modules are more central than others (Mardia, 1972). Finally, we determined the dominant individual's degree of centrality by correlating dominance rank and individuals' centrality between all group members according to Hemelrijk (1998). Our results, in accordance with the egalitarian social system of *M. tonkeana*, showed close proximities among females and juveniles on one side and adults males on the other side, and that the dominant male has a more central position than the females. Compared to methods used in field studies to determine distance between group members (e.g. use of discrete categories), the use of a coordinate system inside the facility allows for more precise results, useful for studying social organization in semi-free-ranging groups.

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## Infection Patterns of Simian Foamy Virus in Macaques

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Within animal groups, social transmission between individuals is dependent on their social interactions and the social structure of the group. More central individuals in their social network are at higher risk of acquiring and transmitting parasites and have more influence on social transmission processes than less central individuals. Investigating the links between host behaviour, parasite transmission and infection risk is paramount in improving epidemiological models and in increasing our understanding of social evolution. In this endeavour, we study simian foamy virus (SFV) in two groups of socially housed rhesus and Japanese macaques (45 and 56 individuals, respectively) at the Primate Research Institute, Kyoto University. SFV is transmitted through saliva and expresses enough genetic diversity to facilitate parasite genotype profiling for individual hosts. We then match these individual profiles to individual (age, sex) and social characteristics (centrality in aggression and grooming networks) to determine more precisely which individuals transmit specific viral strains to other individuals. Preliminary data show that 56/58 adults (>4 years), 30/34 juveniles (1–4 years) and 7/22 infants (<1 year), as well as 63/75 females and 30/39 males tested positive for SFV. Preliminary analyses suggest that individuals more strongly connected in the aggression network, but not in the grooming network, were more likely to be infected. They also indicate that individuals connected to other well-connected individuals (high eigenvector centrality) in the grooming network were less likely to be infected, which may relate to a stronger social support network reducing receipt of aggression. This research can inform animal population management and welfare as well as give insight into evolutionary pressures on sociality and parasitism in animal groups.

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## The Effect of Hot Spring Bathing on Stress Levels in Japanese Macaques

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The ability of primates to survive climatic variation depends on the adaptability of the animals and the configuration of their habitat. Thermoregulatory mechanisms, including behavioural adjustments, help them to maintain homeostasis in response to climate changes. Japanese macaques (*Macaca fuscata*) are the most northerly species of non-human primates in the world and have adapted to live in cold environments. One population is known to use hot springs during cold winter months. Given that thermoregulatory stress can increase glucocorticoid concentrations in primates, we hypothesized that these Japanese monkeys could reduce their glucocorticoid (GC) levels by hot baths. We studied 12 adult female Japanese monkeys (seven lactating, five cycling) living in Jigokudani Monkey Park, Japan, during the birth (April to June) and mating season (October to December) of 2014. Six females did not use the hot springs and the other six were regular bathers. We collected faecal samples from all subjects for determination of GC concentrations by enzyme immunoassay, and behavioural data to determine time spent in the hot springs, dominance rank, and activity budgets. We found that females that take regular hot baths have lower stress hormone levels than non-bathers during the cold winter. Patterns of hot spring bathing by this troop of Japanese monkeys hint that the single hot spring could be a restricted resource favoured by dominant females as a mechanism that not only aids in thermo-

regulation, but also reduces stress hormone concentrations during the winter. Japanese macaques, as in other cold-dwelling mammals, adopt behavioural means of reducing cold climate stress, which could thereby preserve energy for reproduction.

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## Female Androgen Levels, Aggression and Dominance in Wild Verreaux's Sifakas

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While the interactions between androgens, aggression and dominance have been extensively explored in mammalian males, much less is known of these correlations in females. Lemurs are one of few mammalian taxa in which females are often dominant over males, and exhibit high levels of aggression. Nonetheless, few studies have addressed the pathways and interactions between aggression and androgen levels in these species. We collected behavioural and hormonal data on 12 female and 17 male wild Verreaux's sifakas (*Propithecus verreauxi*) in the Berenty Forest Reserve (South Madagascar) across one mating (December 2014–March 2015) and one birth season (June–August 2015). Aggression rates and androgen levels were significantly higher in the mating season than in the birth season, for males and females. While both sexes engaged in comparable rates of aggressive interactions, females had significantly lower androgen levels than males during both seasons. Aggression rates were significantly correlated with androgen levels in males ( $r = 0.54$ ) and females ( $r = 0.45$ ). These results suggest that, in this species, the relationship between female aggression and androgen concentration could follow the pattern predicted by the Challenge Hypothesis (for males), and by extension that male and female proximal mechanisms of aggression might not be so different. We discuss the implications of these findings for our understanding of the evolution of strepsirrhine social systems, and try to reconcile them with those from other lemur species, in which the association between female androgen concentration and aggression was not found.

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## Neuroendocrine Mechanisms of Hunting and Food Sharing in Wild Chimpanzees

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Group hunting and food sharing are collaborative human behaviours thought to play a central role in the evolution of human sociality. Like humans, chimpanzees often engage in group hunting and subsequent meat sharing. During both group hunting and meat sharing, access to benefits is uncertain and relies on coordination and reciprocation. The neuropeptide, oxytocin, associated with trust, coordination and reduced anxiety, plays a role in food sharing in both humans and chimpanzees, and may facilitate this apparently cooperative act on a proximate level. However, since successful hunting often leads to meat sharing, the link between these two cooperative behaviours in relation to the oxytocinergic system is yet unclear. We investigated how the oxytocinergic system is involved in group hunting and food sharing in wild western chimpanzees (*Pan troglodytes verus*) of the Taï forest, Côte d'Ivoire. Using observational data on male and fe-

male hunting, meat and other food sharing, in combination with non-invasively collected urine samples for oxytocin analysis, we found that in chimpanzees, group hunting, meat and food sharing were independently associated with elevated urinary oxytocin levels. We conclude that the oxytocinergic system plays an important role in a variety of cooperative acts in chimpanzees, possibly by facilitating coordination, trust and tolerance during situations involving uncertainty.

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## **Bystander Effects on Grooming Interactions in Western Chimpanzees and Sooty Mangabeys**

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Models of grooming partner choice in primates have largely focused on dyadic relationships between the groomers, based on rank, kinship, and social bonds. However, grooming does not occur in a social vacuum: bystanders may intervene in grooming bouts, alter the market value of each potential partner, and form an audience to whom interactants may signal their fitness and cooperative abilities. It is thus predicted that the audience composition influences when and with whom individuals groom. Further, it has long been argued that species with higher fission-fusion dynamics should be more capable of exploiting the presence and absence of other group members for their advantage. Here, we use western chimpanzees (*Pan troglodytes verus*) and sooty mangabeys (*Cercocebus atys atys*), living sympatrically in Taï Forest, Côte d'Ivoire, as model species with relatively high and low fission-fusion dynamics, respectively. We tested the effect of hierarchy ranks and social relationships between groomers, and the presence of closely- and high-ranked bystanders as well as bond partners of the groomers, on grooming initiations and grooming partner choice ( $n = 1,441$  grooming initiations). Mangabeys initiated grooming more in the absence of high- and closely-ranked bystanders, who might intervene, and in the presence of their own bond partners. The results for the chimpanzee communities were mixed regarding rank, but individuals consistently initiated grooming more when a low number of their own bond partners were present. Individuals in both species preferentially initiated grooming with closely-ranked individuals and bond partners, but also with individuals who had fewer bond partners and closely-ranked bystanders present. Our results indicate that while dyadic variables have a strong impact on grooming decisions, bystander ranks and social relationships influenced grooming initiations in both species.

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## **Identification of Characteristic Behavioural Sequences Reveals Differences in Blue-Eyed Black Lemur and Black Lemur Reproductive Strategies**

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The Critically Endangered blue-eyed black lemur (*Eulemur flavifrons*) and the black lemur (*E. macaco*) are two sister-species for which relatively little is known regarding their reproductive strategies. Over the course of two mating seasons (April–June 2015, 2016), mating activities of focal individuals from the two species were recorded through a combination of continuous and

ad libitum sampling. Temporary male-female dyadic courtships included combinations of vigorous grooming, mate-guarding, mounting, intromission, and post-copulatory grooming. In this study, 81 *E. flavifrons* and 52 *E. macaco* courtships were observed. Of these, 23.1% of *E. macaco* and 13.6% of *E. flavifrons* courtships resulted in copulation. Courtship lengths suggest that *E. macaco* courtships last longer and contain more interactions than those of *E. flavifrons*. We further assessed the occurrence of specific key behavioural sequences for each species using a novel approach, drawing on data mining and bioinformatics techniques. “Male approach” followed by “vigorous allogrooming of female” and “male approach” followed by “mounting of female” sequences were found to occur in at least 25% of *E. flavifrons* and *E. macaco* courtships. More than 25% of *E. flavifrons* courtships contained ‘male mounting’ followed by “female aggression” or “female disengagement”; these sequences occurred in *E. macaco* less than 10% of the time. While “male scent marking a female” and “male mate-guarding a female” sequences were found to occur in at least 25% of *E. macaco* courtships, fewer than 10% of *E. flavifrons* courtships contained these sequences. These findings suggest that despite a close phylogenetic relationship, *E. flavifrons* and *E. macaco* are displaying unique mating strategies. The analysis of sequential interactions can further be applied to other primate species not only to elucidate characteristic patterns of reproductive behaviours, but also to provide insight into hybridization probabilities in areas of species sympatry.

## Oral Communications Manipulation & Locomotion

### A Novel Approach to Study Activity Patterns of Cryptic Primates: Unsupervised Learning Algorithm for Data from Three-Axis Accelerometer Tags

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Activity of primates has been mostly assessed via behavioural observations. More recently, primatologists have introduced the use of loggers that estimate percentage of activity based on cumulative locomotor counts. In other animals, researchers used three-axis accelerometer tags that store raw data at high frequency on X, Y, Z variations and have larger storage memory than loggers based on activity counts. This allows the extrapolation of more fine-grained data on the animal's activity. One way to analyse these data is based on supervised learning algorithms that work on manually selecting behaviours and extrapolating the activity patterns based on direct observations. Another approach, recommended for latent behaviours, is the unsupervised learning algorithm that statistically groups accelerometer data into different categories of behaviours. We tested the use of an unsupervised learning algorithm to extrapolate information on activity patterns of two nocturnal lemurs, *Avahi meridionalis* and *Lepilemur fleuretae*, in the lowland rainforest of Tsitongambarika, south-east Madagascar. In particular, we tested the efficiency of the unsupervised Expectation-Maximization (EM) algorithm in extrapolating percentage of activity and specific behaviours (feeding and locomotion behaviours) by comparing the estimates with direct observations. We recorded data every second for four months on four individuals of *A. meridionalis* and three individuals of *L. fleuretae*. For the EM algorithm we calculated the OBDA vector (sum of the dynamic acceleration on the three axis) and the Pitch (vertical orienta-



tion of the body angle), with the Bayesian information criterion to select the best model. Overall, the EM algorithm fitted with the behaviours observed on the two species. We conclude that, for cryptic animals such as nocturnal primates inhabiting rainforests, the use of unsupervised learning algorithms can provide fine-grained information that is not possible to collect in other ways.

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## Pedal and Manual Postures during Locomotion on Various Substrates in Strepsirrhine and Haplorhine Primates

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Grasping extremities are among the defining features of primates and are central for understanding their origins and early evolution. More particularly, a foot, with an opposable hallux and nails on all digits specialized for powerful grasping is a key feature which is functionally associated with fine branch utilization that purportedly promoted early primate differentiation. However, the evolutionary context of these unique adaptations and the ancestral primate morphotype remain under debate. In this context, the study of pedal (and manual) grasping strategies in relation to substrate diameter and orientation are central for understanding the mechanical constraints that are functionally linked to these morphological specializations. In this study, we investigated the influence of substrate characteristics on foot and hand postures during locomotion in primates. For these purposes we quantified detailed postures in 4 strepsirrhines (*Haplemur griseus*,  $n = 1$ ; *Eulemur mongoz*,  $n = 1$ ; *E. coronatus*,  $n = 4$ ; *E. rubriventer*,  $n = 4$ ) and 3 haplorhines (*Saguinus imperator*,  $n = 4$ ; *Saimiri boliviensis*,  $n = 4$ ; *Callicebus cupreus*,  $n = 5$ ) in semi-natural conditions. Preliminary results show that foot postures appear less diversified than hand postures, for all species and substrate categories. Concerning the foot, all species preferentially used hallucal grasp on all substrates, but haplorhines exhibited a high proportion of non-grasping postures with the foot positioned parallel on medium and large substrates. Haplorhines also exhibited a lower degree of opposability than strepsirrhines. Regarding the hand, strepsirrhines and the haplorhine titi monkey (*C. cupreus*) demonstrated high use of the zygodactylous grasp. If haplorhines are closer to the ancestral primate morphotype for hand and foot morphology, our results could question the role of fine branch use in the evolutionary acquisition of nails in early primates.

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## Consistency in Preferential Hand Use by Captive Chimpanzees (*Pan troglodytes*) in Five Motor Tasks Involving Tool Use and in Manual Digging

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Chimpanzees show hand preference at the individual level in a wide variety of manipulative tasks, but few studies have investigated the consistency in hand preferences across tool use tasks. The aim of our study was to assess hand preference in six tasks performed by nine captive chim-

panzees living as a group at Kristiansand Zoo in Norway. We studied five motor tasks involving tool use (honey extracting, tube task, puzzle feeding, artificial termite fishing and tool digging) and, for comparison, one non-tool use task (manual digging, for which hand preference has never before been directly assessed). Our results show that manual digging elicited significant hand preference in seven of eight individuals. The ratio of individuals showing significant left-hand preference: no-hand preference: right-hand preference in this task was 2:1:5. Hand preferences were less evident in the tool use tasks. The lowest proportion of chimpanzees showing a significant hand preference was found in the tube task (1:5:1). Regarding consistency in hand preference, only one individual consistently used the same hand across all tasks he participated in, five individuals showed a hand preference only in certain tasks but with consistent direction (left or right), and three individuals showed switches in the preferred hand depending on the task type. Individual hand preferences appear to be strongly dependent on the type of task, and are apparent for both tool tasks and a non-tool task. Manual digging elicited strong hand preferences in the chimpanzees that participated in the task, which differs from the results of previous studies that found manual digging to be ambidextrous based on indirect evidence. The degree of consistency in hand preferences varied between individuals, the direction was consistent in six of nine subjects and the three individuals that were inconsistent, presented different directions of hand preference in the manual task compared to the tool use tasks. Taken together, the present findings suggest that chimpanzees do not display the same high degree of consistency in hand use across tasks which is typical for human handedness.

## Oral Communications Ecology

### The Energetics of Reproduction in a Wild Malagasy Primate

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Is reproduction energetically costly, and do these energy costs underlie variation in fertility? In primates with dilute milk and long lactations for their body size, the interaction of energetics and reproductive rates remains the subject of considerable debate as to mechanisms and costs. Despite the long-held view that reproduction is a costly activity, there have been only a few studies to date directly assessing energy expenditure in free-ranging primates. Malagasy primates inhabit a highly variable environment with a lot of fluctuations in food availability, and females must develop cost-effective strategies to regulate their energy balance while facing harsh seasonal conditions and reproductive costs. Here, we explored the relationship between nutritional status, total energy expenditure (TEE) at the beginning of the mating season and reproductive outcomes, using doubly-labelled water and morphometric measurements in nine wild female sifakas (*Propithecus verreauxi*) of 9 groups (i.e. 1 sampled female per group) in Berenty Reserve, South Madagascar (2014–5). Our results indicated that estimated percent body fat was relatively low (mean  $\pm$  SD = 7.0  $\pm$  2.6%). Among morphometrics, body mass provided the best predictor of fat-free mass and fat mass, and we also found a strong positive relationship between fat-free mass and thigh circumference. TEE tended to be positively correlated with crown-rump length, with longer females expending more energy on a daily basis than did shorter ones. We found a

relationship between conception rates and energetic condition, with females that conceived being in better condition (higher Quetelet Index) at the beginning of the mating season than those who did not conceive. Moreover, fat mass was significantly correlated to birth date, with fatter females giving birth later in the birth season. These results suggest that females with higher energy status could invest more in reproduction and could afford to reproduce more efficiently.

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## First Evidence of Geophagy in a Free-Ranging Group of Yellow-Tailed Woolly Monkeys (*Lagothrix flavicauda*) in La Esperanza, Peru

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Geophagy is the deliberate ingestion of soil and has been observed in many species, including humans. It is most often described as a behaviour allowing nutritional supplementation, improving digestion, detoxification of secondary metabolites and/or self-medication. This study provides the first records and observations of geophagy in the yellow-tailed woolly monkey (*Lagothrix flavicauda*), a Critically Endangered (IUCN Red List, 2016) and little studied primate species endemic to a small region of pre-mountain and mountain cloud forest between 1,500 and 2,700 m above sea level in Peru. Our work aims at highlighting the role of this particular behaviour in the feeding ecology of *L. flavicauda*. We hypothesize that frequencies of geophagy could be correlated to consumption of other food types. During our field missions, data were collected to compare how seasonal effects may influence individual food strategies and geophagy behaviour. Geophagy was determined through camera traps and direct observations. Feeding behaviours were collected through focal animal sampling on 1 group of 20 individuals. We recorded, for each age and sex classes, i.e. adult male, adult female, juvenile female and juvenile male, the species consumed, the food type, i.e. fruit, leaf, petiole, flower, dry trunk, insect found in epiphyte, and the maturity of vegetal items. When we recorded at least two consecutive data points of feeding in the same tree, we marked and georeferenced the tree as a “feeding tree.” Chemical analyses, i.e. soil characterisation and microelement availability, were conducted on consumed and non-consumed soils. Our results suggest that occurrences of geophagy in *L. flavicauda* could be related to a higher consumption of leaves. Moreover, preliminary soil analyses revealed a higher concentration of clay in consumed soils. This study provides fundamental knowledge on the ecology of this species and could contribute to improving its conservation. Indeed, our results on geophagy in *L. flavicauda*, provide additional knowledge about the needs of this species and its use of its territory. This information should be included in community conservation plans in our work area where deforestation and soil use by local people represent the highest threats to the survival of this species.

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## **Behavioural Flexibility of Vervet Monkeys (*Chlorocebus pygerythrus*) Living in a Savannah-Woodland Fragment in Tanzania**

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Primate habitats are being increasingly disturbed by human activities worldwide. The behavioural flexibility exhibited by vervet monkeys (*Chlorocebus pygerythrus*) is assumed to be crucial for the species' ability to persist in habitats heavily altered by humans. To increase our understanding of this species' behaviour and ecology, two neighbouring groups of vervet monkeys living in areas with different degrees of human disturbance were studied in a savannah-woodland fragment in Tanzania. The activity patterns, diet and ranging patterns of both groups were investigated. The group occupying the less altered area spent significantly more time moving, while the one occupying the most altered area spent significantly more time foraging, playing and engaged in sexual activity. The overall home range size (95% fixed Kernel Density Estimation) and mean daily travel distance were greater for the group occupying the less altered area. The group living in the most altered area included a larger number of food species in their diet, ate significantly more fruits and human derived (cultivated and processed) foods while the group living in the less altered area ate significantly more seeds and wild foods. The vervet monkeys in this study used flexible strategies to obtain food, mainly to access the human derived food available in their habitat. Conservation strategies need to be implemented to prevent the potential increase of the human-monkey conflict, which will compromise the long-term survival of the vervet monkeys in this fragmented habitat.

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## **Lemur Abundance in the Lowland Rainforest of Tsitongambarika, Southeastern Madagascar: Altitudinal and Latitudinal Comparisons**

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Altitude and latitude are two factors that notoriously affect primate diversity and abundance. Primates living at low elevation benefit from high plant diversity, and this often leads to higher species diversity than in mid and high altitude habitats. A similar reasoning is used for latitude, with decreasing diversity observed with increasing distance from the equator. Lemur species richness in eastern rainforest habitats has been found to reach its maximum in central Madagascar between ca. 800 and 1,200 m, which represents a higher elevation compared to sites outside the red island. This phenomenon has been explained by the limited expansion of the lowland rainforest on the island and its expansion-contractions over time. However, studies focusing on lowland rainforests in Madagascar are scarce and species niche breadth not well defined. In this study we compared new data on diversity and abundance of lemurs inhabiting one of the largest expanses of lowland rainforest in south-eastern Madagascar, the Tsitongambarika Protected Area. Being south of the Tropic of Capricorn, the area also represents one of the southernmost rainforests in the country. The results were compared with data from con-generic species from rainforests at different altitudes located further north on the island. We estimated population abundance from 9 transects of 1 km, which were walked once a month during the day and at night from May 2015 until July 2016. In total we walked 125 km during the day and 96 km at night. Estimated abundance of folivorous, nocturnal genera, *Avahi* and *Lepilemur*, were high

compared to other areas, while the abundance of *Microcebus*, *Eulemur* and *Haplemur* was comparable to other sites. Overall, the low altitude rainforest of Tsitongambarika seems to host high densities of folivorous lemurs than mid- and high- altitude rainforests. As expected from its southern latitude, the overall lemur diversity was lower compared to rainforests closer to the equator. Decreased competition and niche expansion due to low lemur diversity and biogeographic dynamics are proposed to explain these results.

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### Energy Expenditure and Body Composition of Verreaux's Sifakas in Forest Fragments of the Arid South of Madagascar

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The ability to store fat has been hypothesized to have a strong impact on the fitness value of primate species living in highly seasonal environments such as southern Madagascar. In the Verreaux's sifaka (*Propithecus verreauxi*), fat storage may be in anticipation of the long period of food shortage occurring during the dry season and/or a way to cope with the energy demands of the mating season, which is strictly seasonal in this species. Seasonal variation of body mass has been extensively documented in this folivorous lemur, but it is unclear whether this reflects changes in fat mass or lean mass linked to changes in physical activity. Here, we determined nutritional status, body composition, and total energy expenditure (TEE) during the mating season using isotope-labelled water and morphometric measurements in 24 adult sifakas (15 males and 9 females). The nine focal groups lived in two types of forests categorized according to their more or less anthropogenic nature and distinct richness in preferred food sources (Berenty Reserve, South of Madagascar). Analysis of variance showed that body mass, fat-free mass, thigh muscle thickness and thigh circumference were higher in "anthropogenic forest" groups ( $n = 5$ ; 12 individuals) compared with "natural forest" groups ( $n = 4$ , 12 individuals;  $p < 0.001$ , except for thigh muscle thickness:  $p < 0.05$ ). The proportion of fat mass did not differ between these groups ( $p = 0.34$ ), nor did the length of body segments (trunk, tail, thigh tendon length;  $p = 0.32$ ,  $p = 0.42$ ,  $p = 0.78$ , respectively). This indicates that variations in body weight between individuals are primarily due to differences in musculature, especially that of the hind limbs. We also found that TEE was correlated with body mass ( $p < 0.04$ ), while sex and forest type had no effect on it. We discuss the variation of TEE and body composition in relation to the level of physical activity, diet, and the locomotion effort imposed by the different forest structure and sifaka density of the two habitats we considered.

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## Exploring Niche Partitioning in Strepsirrhines: *Lepilemur fleuretae* and *Avahi meridionalis* in the Lowland Rainforest of Southeastern Madagascar

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The possession of largely similar habits leads to partial niche overlap between species, which may compete if the resources used are in limited supply. The sympatric lemur genera *Lepilemur* and *Avahi* are ecologically similar since both are nocturnal, folivorous and have a comparable body weight. *Lepilemur* has a lower diet quality when in sympatry with *Avahi*, thus a possible competitive exclusion has been hypothesised. Previous comparative studies in deciduous forests found limited niche overlap in *L. edwardsi* and *A. occidentalis*, with differences in food selection and social structure. Little is known about niche separation in the eastern rainforest, which is the largest habitat where the two genera occur sympatrically. This study aims to assess the ecological niche partitioning of the Critically Endangered *L. fleuretae* and the Endangered *A. meridionalis* in the Tsitongambarika lowland rainforest, southeastern Madagascar. We collected year-round data (July 2015–July 2016) on habitat use, activity patterns, and diet via continuous sampling on 6 individuals of *L. fleuretae* (139 h) and 6 individuals of *A. meridionalis* (148 h). We used one-way ANOVA to compare data between the two species. *L. fleuretae* fed and moved at greater heights than *A. meridionalis*. *A. meridionalis* had more crepuscular activity than *L. fleuretae*, while *L. fleuretae* had more activity at night. *A. meridionalis* and *L. fleuretae* fed on 45 and 31 different food items respectively, with 15 food items in common. *A. meridionalis* was strictly folivorous, while *L. fleuretae* was mainly folivorous (78.8%) but integrated flowers (11.0%), fruits (9.9%), and insects (0.3%) into its diet. Overall, the two species showed mechanisms of niche partitioning in the three niche dimensions (diet, habitat use and time). Thus, we can exclude competitive exclusion between the two genera. In conclusion, it is crucial to consider several levels of niche partitioning to assess fine-grained differences among species.

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## Orangutan Population Structure in a Marginal Habitat and Its Implications for Conservation

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Most long-term wild orangutan studies are based on stable resident populations, living in forests with relatively high fruit productivity, characterized by female philopatry, male dispersal, and male nomadism. It is not known whether orangutans living in exceptionally unproductive habitats exhibit the same patterns. We therefore studied wild Bornean orangutans (*Pongo pygmaeus morio*) living in the intact, mostly undisturbed dipterocarp forest of Wehea Protected Forest, East Kalimantan, from May 2014 to December 2016. This forest may represent some of the most consistently fruit-scarce orangutan habitat across their geographic range. Using monthly phenology monitoring ( $n = 27$  months), nest surveys ( $n = 20$  months), and direct encounter rates ( $n = 192$  search team days), we show that orangutan population density is very low and does not directly correlate with variation in fruit availability. Furthermore, direct encounter data and camera trap records ( $n = 2510$  camera trap days over 7 months) reveal an exceptionally low re-encounter rate of individually identified orangutans ( $n = 34$  identified individuals;  $n = 3$  individuals re-encountered more than once). Unlike other orangutan populations in which females maintain

stable long-term home ranges, only 1 (of 4) identified adult female was present for >1 year in our study area, and even she was sometimes absent from the area for long periods of time. The data suggest that in such naturally poor quality habitat as Wehea, orangutans maintain exceptionally large, dynamic home ranges (in the case of some females) and nomadic or migratory ranging strategies (in the case of males and other females). As such, orangutans may be using this low-quality habitat predominantly as a corridor between higher quality – but also highly variable – habitats. These findings have important implications for conservation initiatives, including land-use planning, as well as translocation and reintroduction programmes.

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### ***Dialium* and Seed Reingestion from Faeces in Western Gorillas: A Source of Protein and “Cooking” Effect**

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Unraveling the relationship between the nutritional intake of endangered species and their unusual feeding behaviours may provide crucial information for understanding their response to seasonal and unpredictable variation in food availability in their environments. Primates sometimes re-ingest fruit seeds from faeces (coprophagy). We investigate the ecological correlates of coprophagy in wild western gorillas (*Gorilla gorilla*), particularly testing if it occurs during periods of lower fruit availability and if it leads to higher nutrient intake. Data included behavioural observations collected at two field sites in Central Africa (Mbeli Bai: ad libitum observations based on 11,511 h; Bai Hokou: 720 h of 5-min scans on focal animals from December 2004–December 2005), phenological records, faecal sample inspections and nutritional analysis of food items. Gorilla coprophagy occurred at the end of the high-fruited season and correlated positively with the presence of *Dialium* spp. in gorilla dung and feeding bouts of *Dialium*, as well as *Dialium* fruit availability. *Dialium* seeds have very high levels of protein content and of phenols and tannins compared to other gorilla food items. This suggests that coprophagy in western gorillas may be linked to a search for protein. The gut processing likely improves their ability to extract macro- and micro-nutrients while concurrently softening indigestible fibre and reducing antifeedant content. In this sense, coprophagy by western gorillas can be regarded as having a ‘cooking’ effect on seeds, helping to increase nutrient intake while concurrently decreasing the effect/presence of secondary compounds.

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### **New Evidence of Well Digging in Savannah Chimpanzees (*Pan troglodytes schweinfurthii*), Kahensa, Tanzania**

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Surface water can be scarce in savannahs during the dry season, posing a challenge to chimpanzees in these habitats. In a few study sites, chimpanzees have been reported to access drinking water by digging holes (“wells”) in sandy riverbeds. However, chimpanzees can also make these wells near sources of running water, presumably to filter this liquid. Chimpanzee well digging behaviour is most frequent during the dry season. In Semliki, Uganda, chimpanzees sometimes use



leaf-spoons or sponges made of vegetation to extract the water from the bottom of the wells. Here we report on new evidence of savannah chimpanzees digging wells to obtain water. These data come from Kahensa, a new study site in Ugalla, western Tanzania, one of the driest, most open and seasonal habitats where chimpanzees exist. The chimpanzees were not habituated to human observers, but we inferred they were the excavators of the holes based on the indirect evidence they left at the digging sites: knuckle and footprints and tools (sponges made of leaves) associated with the holes. For each hole, we measured the maximum length, width and depth and recorded the presence of water inside the cavity and the number of associated leaf sponges. We found a total of 20 wells along one streambed. Eleven wells had at least one leaf sponge close or inside the cavity. We found no evidence of tools used for digging the wells. The only associated tools were the leaf sponges, inferred to have been used to extract the water from the wells. We discuss the implications that our finding has for understanding the adaptations of chimpanzees to savannah habitats.

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### Seasonal Variation in Indicators of Climatic and Ecological Stress in Savannah-Dwelling Chimpanzees

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Located at the northwestern edge of the West African chimpanzee's (*Pan troglodytes verus*) range, the Fongoli chimpanzee community endures the climatic extremes within the species' range. This extreme but seasonal environment elicits otherwise uncommon thermoregulatory behaviours, such as pool and cave use, as a way of mitigating the burden of living in an arid and open environment. Here we examine to what extent potential environmental stressors physiologically affect Fongoli chimpanzees. Specifically, we investigated whether there was seasonal variability in energy balance, hydration status, and heat exposure. We then examined whether this variability was correlated to cortisol levels. We collected urine samples ( $n = 368$ ) over an annual cycle (beginning in January 2013), with which we measured seasonal variation of creatinine, c-peptide, and cortisol in adult individuals, as measures of water, food, and heat constraints, respectively. We evaluated the effect of individual characteristics and various phenological, climate, and behavioural parameters on the aforementioned biomarkers. Results illustrated significant seasonal variation in both creatinine and c-peptide, which corresponded with relevant ecological factors. Additionally, cortisol values showed significant seasonal variation correlating to high temperatures, even while controlling for the seasonal variation of the two aforementioned indicators. We observed a significant relationship between creatinine and cortisol levels, however no such relationship with c-peptide and cortisol levels was found. These results, therefore, suggest that Fongoli chimpanzees endure periods of heat and hydration stress, but are able to avoid stressful levels of negative energy balance.

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### Survey of Chimpanzees, *Pan troglodytes verus* (Schwarz, 1934), Outside the Protected Areas in Senegal (West Africa)

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The West African subspecies of chimpanzee, *Pan troglodytes verus*, is Critically Endangered. In Senegal, more than 70% of chimpanzees live in the hot, dry and open savannah outside the na-

tional park system. The number of chimpanzees in this country is estimated to number fewer than 500 individuals but much of this area has not been extensively investigated. For this reason, we surveyed chimpanzees in unprotected areas of the Kedougou region of southeastern Senegal between November 2014 and July 2015. We conducted recce walks ( $n = 57$ , 300 km total) through confirmed and potential chimpanzee habitats to observe chimpanzees and indices of chimpanzee activity, such as sleeping nests, tracks, and faeces. We accumulated 21 direct contacts with chimpanzees and recorded 3,489 chimpanzee nests. We mapped the geographical distribution of chimpanzees sleeping sites and indicators of anthropogenic activities to facilitate species management and conservation planning in the immediate future. In addition, we identified the habitats and tree species used by chimpanzees to construct their nests in order to explore nesting tree preferences. Chimpanzees used almost 40 tree species in the Kedougou region, but 60% of their nests were found in only three tree species: *Pterocarpus erinaceus*, *Diospyros mespiliformis* and *Anogeissus leiocarpus*. Moreover, chimpanzees nested more often in woodland habitat than in gallery forests, although the latter is a crucial habitat for chimpanzees, perhaps because gallery forest accounts for a small percentage of available habitat in southeastern Senegal. Thus, particular attention is needed for the management of these tree species for a good conservation of chimpanzees in this region. In addition, it would be useful to produce a local action plan for these savannah chimpanzees in this hot and dry habitat.

### **Nesting Patterns of Chimpanzees (*Pan troglodytes verus*) in a Savannah Habitat, Dindefelo, Senegal**

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It has been hypothesized that the elevated height of a chimpanzee nest is a predator defense strategy. But even though nesting behaviour has been studied since the earliest field studies of chimpanzees, the anti-predator function of nests remains poorly understood. We investigated the nesting patterns of chimpanzees (*Pan troglodytes verus*) at Dindefelo in Senegal, a savannah site where human activity is present, with the aims of: (1) detecting environmental influences on nest building, (2) identifying the physical characteristics of trees preferred by the chimpanzees for nesting, and (3) testing the anti-predator hypotheses of arboreal nesting. We examined the physical characteristics of 323 nests and 202 trees used for nest construction. The majority of the nests were built in the middle section of the tree crown and close to the tree trunk. Over one third of the nests were constructed using more than one tree. In addition, to assess further the patterns of selectivity by the chimpanzees, the physical characteristics of trees used for nesting versus trees not used for nesting (despite being of suitable dimensions) were systematically compared. Our results show that the chimpanzees preferred trees that were taller, had a larger trunk diameter, taller and wider crown, larger leaf size and more escape routes compared to non-nesting trees, giving support to the hypothesis that chimpanzees select specific trees based on characteristics that help to avoid predation. However, predator pressure at Dindefelo seems to be low and we found ground nests, albeit rarely. Further data are needed to more adequately test the hypothesis that the elevated height of a sleeping place is an anti-predator strategy at Dindefelo. Human activities within the study site may affect the availability of plant resources vital for the chimpanzees to construct their nests and constrain their choices. Given the current critically endangered status of *Pan troglodytes verus*, our findings contribute to understanding how chimpanzees adjust their nesting behaviour to changes produced by human activities and have important implications for designing conservation strategies to protect their nesting resources.

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## **The Relationship between Food Distribution and Contest Competition: Evidence from a Non-Primate Species, the Asian Elephant, in Southern India**

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A core prediction of the socioecological theory that explains inter-specific variations in social relationships amongst females is that food abundance and distribution define the competition regime which affects within-group and between-group dominance interactions. As data to test the theory largely come from primates, there have been demands for extending the empirical tests to non-primate mammalian taxa to explore the generality of the predictions. In this study, we test some ecological predictions regarding contest competition in female Asian elephants in southern India. Data were collected from short grass habitat around the backwaters of the Kabini reservoir in the dry seasons of 2015 and 2016. Although food-related contests are often not expected in such habitats, as grass is assumed to be a low quality food type, studies on primates have cautioned against the generalization of food distribution (i.e. clumped or dispersed) from diet type (e.g. frugivory or folivory). We, therefore, quantified food distribution by weighing harvested grass biomass in different demarcated zones (focal zones) of the backwaters and in the surrounding forests. We present data on the relationship between grass biomass distribution and intensity of contest competition. Grass biomass in the Kabini grassland was 3–4 times that of the biomass in the adjacent forest landscape indicating that Kabini backwaters is a resource-rich patch surrounded by forests with low grass abundance. Grass biomass was also significantly different across focal zones within the grassland. This patchy and heterogeneous resource distribution possibly explains the intense between-group contests observed in this area. We further found substantial local heterogeneity in grass abundance within focal zones, which may have implications for within-group contests. Similar to the pattern seen in primates, these results show that patchiness of food resources (rather than diet type alone) results in contest competition. We discuss how assessments of resource distribution can help us understand the robustness of predictions from socioecological theory in the proboscidean clade.

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## **Spectral Niche Segregation in Sulawesi Dawn and Dusk Choruses: The Place of Tarsiers and Small Mammals**

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Abstract not available.

## Oral Communications

### Communication

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#### Linguistic Laws in Chimpanzee Gestural Communication

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A number of recent studies have tested whether the statistical laws of human language – known as linguistic laws – are also seen in primate vocal communication. It has been found, for example, that calls in the vocal repertoire of Formosan macaques, *Macaca cyclopis*, follows Zipf's law of abbreviation (which predicts a negative relationship between signal length and frequency of use), and that the vocal sequences of geladas, *Theropithecus gelada*, follow Menzerath's law (according to which longer sequences are made up of shorter constituents). Both laws have been mathematically linked to compression, the information theoretic principle of minimising code length, and it has been argued that this phenomenon underpins diverse biological information systems, reflecting a universal pressure for coding efficiency. Here we present the first test of linguistic laws in primate gestural communication. Analysing video recordings of the play gestures of 48 wild chimpanzees, *Pan troglodytes*, in Budongo National Park, Uganda, we found a strong negative relationship between number of gestures in a sequence and mean duration of the constituent gestures (in line with Menzerath's law) but no relationship between mean gesture duration and frequency of use (contrary to Zipf's law of abbreviation). However, analysis of specific subsets of the overall gestural repertoire revealed strong agreement with Zipf's law of abbreviation, demonstrating that patterns consistent with this law were hidden when the entire repertoire was analysed. Our results provide evidence that compression underpins the pattern of use of individual play gesture types and the construction of play gesture sequences, indicating this principle applies across different modes of primate communication.

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#### Gestural Communication in Olive Baboons (*Papio anubis*): Repertoire and Properties

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Given their close phylogenetic proximity with humans, non-human primates can be used as models to investigate the evolution of advanced communicative systems. In this regard, there is renewed interest in studies concerning gestural communication. In apes, it has been shown that

the production of gestures is intentional (e.g. the gestures are adjusted to the attentional state of the recipient), flexible (e.g. the same gesture can be used in several contexts), and variable across individuals and populations. However, compared to apes the gestural communication of monkeys has been understudied. It is thus important to establish which gestures are used by monkeys and to investigate whether their gestural system possesses the same properties as the gestural system found in apes. In this study, we investigated the gestural communication of 47 captive olive baboons of all ages living in 3 social groups. We used a focal sampling approach to observe each subject for a total of 5 h spread over one year. For each signal produced by the focal subject toward a recipient we recorded its physical description, the orientation of the signaller, the attentional state of the recipient, the situational context and the response of the recipient. We collected a total of 2820 focal sessions, corresponding to 60 sessions of 5 min for each subject, and established a preliminary list of 65 signals produced by the baboons. Preliminary results indicate that 91% of the signals were produced when the signaller was looking at the recipient and 85% when the recipient was attending. The data will be further analysed to investigate in detail the properties of the signals, notably in terms of intentionality, flexibility and variability. This study represents the first systematic investigation of the gestural communicative system of olive baboons and the results will be compared to the gestural system described in apes.

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## The Informative Value of Recipient and Signaller Disagreement for the Study of Intentional Communication in Wild Chimpanzees

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Intentional communication in non-human primates is often analyzed solely from the perspective of the signaller. The recipient's reaction to a possible intentional production from the signaller is then largely ignored. In this framework, situations where no communication between the two occurs, or where recipients make decisions independent of the signaller's potential goal and the signal's intended meaning, may qualify as instances of intentional communication. The key to excluding these instances is to explicitly focus on recipient's reactions and signaller's responses, that is on their communicative interaction. Particularly, cases where producer and recipient disagree are informative because both actors can provide clues to their disagreement by indicating a diverging goal or displaying dissatisfaction. Do wild chimpanzees display such communicative disagreement? To explore this question, we video-recorded travel initiations in wild chimpanzees (*Pan troglodytes schweinfurthii*) in Budongo Forest, Uganda, using focal animal sampling over a 6 month study. We were particularly interested in instances where 1 individual had the goal of leaving with a recipient, but the recipient did not follow and therefore both engaged in a back and forth interaction including turn taking. We found 21 occurrences of such conflicts of interest out of 283 travel initiations (7%) in various contexts including family travel and courtship. To analyze these instances, we studied the orientation of the body, the moves and gazes of the partners towards the travel direction and each other, and whether they displayed aggression or extensive waiting. We describe these cases and analyze how chimpanzees rely on various modalities including vocalizations and gestures to reach a common outcome. Our data show that wild chimpanzees are capable of communicating and negotiating diverging goals during travel, though this remains rare.

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## Macaques Are Less Likely to Attack Others Producing Stress Behaviour

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Primates (including humans) scratch when stressed. So far, such scratching has been seen as a by-product of physiological processes, and attributed proximate, regulatory function. However, it is possible that there is an additional adaptive function of producing an observable behaviour when stressed. Here, we tested the social responses to scratching in a group of free-ranging rhesus macaques (*Macaca mulatta*). We followed 45 adult monkeys, recording all occurrences of stress related, and social behaviour through focal-animal sampling. We show that when macaques scratch, they are less likely to be the target of aggression. Stress could therefore have evolved as an observable phenomenon by reducing the potential for escalated aggression, benefiting both senders and receivers by facilitating social cohesion. Sensitivity to the internal states of others, including stress, may reduce social uncertainty and allow for more coordinated interaction in the future. Or it could be that attacking stressed individuals may be a risky and/or unnecessary action as stressed individuals could behave unpredictably or be weakened by their state of stress. Importantly, this basic ability to recognise stress in others could provide an essential evolutionary step towards more complex social cognition such as empathy.

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## Specific Facial Replications in Chimpanzees and Orangutans during Social Play

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Facial replications reflect the capacity to match facial expressions, whether they are voluntarily or involuntarily produced. They represent an important phenomenon of non-verbal communication and are argued to promote social cohesion in both humans and non-human primates. In humans, even specific variants of facial expressions may be replicated as we are able to subtly alter our facial expressions to match those of others, i.e. specific facial replications. The current study, thus, assessed whether great apes share this ability. To do so, we examined the specificity of facial replications in 23 chimpanzees, *Pan troglodytes*, from Chimfunshi Wildlife Orphanage (Zambia) and 27 rehabilitated orangutans, *Pongo pygmaeus*, from Sepilok Rehabilitation Centre (Malaysia) in face-to-face interactions during spontaneous dyadic play. Two variants of open-mouth laugh faces were coded during dyadic social play: one variant with only the lower teeth exposed and the other variant with both the upper and lower teeth exposed. The results revealed that chimpanzees and orangutans replicate the facial expression of their social partners by producing the same facial variant during play, highlighting a more complex form of facial communication than previously known for great apes. Consequently, humans are not unique in this subtle positive facial communication that perhaps further supports social cohesion. This study brings new insights about deep evolutionary roots of complex non-verbal communication in the primate lineage.

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## The Timing of Vocal Accommodation in Common Marmosets (*Callithrix jacchus*)

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Vocal accommodation is a phenomenon where interactants modify their vocalization according to current interaction partners. It provides information about the social relationship of partners, and can take the form of convergence (becoming more similar, indicating social closeness) or divergence (becoming less similar, indicating social distance). The phenomenon is well studied in humans but less is known about it in non-human primates (NHPs). In particular, little is known about the onset, temporal pattern and changes in accommodation in NHPs. We studied vocal accommodation in common marmosets to analyse its temporal pattern while taking previous vocal similarity of partners into account. We collected vocal recordings of 10 captive, newly-formed breeding pairs. We collected calls before the introduction as well as over the first 9 weeks of the pair formation process to measure whether the pairs converged in their call structures. Further, we collected data on social behaviour like proximity, grooming and food sharing over this time to estimate pair bond strength, social closeness and individual investment in the pair bond. We analysed three social call types (phee calls, trill calls and food calls) and measured 16–18 parameters per call (depending on call type). To estimate similarity between partners, we calculated Euclidian distances between the calls of partners at different time points and compared the differences using randomized *t* tests. We find significant evidence for vocal accommodation in common marmosets in at least one call type, the trill call. First results show that the temporal pattern of accommodation varies between pairs, but occurs within the first few weeks after introduction. For some pairs, accommodation occurs only during the first 2–3 weeks, while other pairs show accommodation up to week 9. Results show that pairs can both converge and diverge over the course of pair formation. These results highlight the vocal flexibility of common marmosets and indicate their vocal learning abilities. The relationship between accommodation and pair bond quality is currently under investigation.

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## Identity and Contextual information in Alarm Calls of Titi Monkeys

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Titi monkeys (*Callicebus nigrifrons*) produce two acoustically simple alarm calls, the A- and B-calls. A-calls functionally refer to threats within or above the canopy, such as raptors and capuchin monkeys. B-calls are given in a broader context, which includes terrestrial predators, when the caller is moving near the forest ground or when disturbed by humans, suggesting that B-calls refer to dangers emanating from the ground. The common observation that primate terrestrial alarm calls are contextually broad has led to questions about whether such calls should be termed functionally referential. In this study, we collected A-calls emitted in two contexts (presence of capuchins or aerial predator) and B-calls from three contexts (presence of a terrestrial predator, human disturbance, monkey near the ground) from six wild groups of titi monkeys in the Santuário do Caraça, Brazil. We ran acoustic analyses and found that both A- and B-calls can be statistically discriminated into different acoustic variants in relation to their context of emission, and that both call types were individually distinct. Our study thus suggests that even acoustically simple alarm calls, such as the ones of titi monkeys, can convey additional information about specific contexts beyond a simple terrestrial/aerial distinction. Moreover, our findings sug-



gest that the apparent lack of specificity of the terrestrial alarm call may be resolved at the level of call variants. Playback experiments will be needed to confirm that differences in call variants are perceived by recipients before further conclusions can be made about the referential nature of these alarm calls.

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## The Evolution of Crying: Distress Calls and Infants' Needs in Wild Chimpanzees

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Distress calls are the most primitive mammalian vocalizations. They appear early in ontogeny and are highly preserved in phylogeny, with a simple structure also present in species beyond the Mammalia class. Although the general evolutionary function of distress calls is well determined (attention from caregivers), the diversity of vocal behaviours belonging to this broad category requires a more thorough examination. In particular, it is unclear how the various acoustic types pertaining to this vocal class are related to biological function. For chimpanzees, there has been no detailed inventory of the types of calls produced by infants when distressed. Given the complexity and length of mother-infant interactions in this species, as well as the wide range of parent-offspring conflicts, we predict considerable acoustic flexibility in the distress calls of young chimpanzees (the hoos, whimpers and cries). To this end we examined different factors that may explain the acoustical variation in distress calls of 8 young chimpanzees (*Pan troglodytes schweinfurthii*) of the Sonso community, Budongo Forest, Uganda, during natural interactions with their mothers. We extracted critical physical features from the acoustical recordings, and trained a classifier (support vector machine (SVM)) to create a model that separates best the resulting feature vectors according to class labels (e.g. whether the mother approaches the infant or not upon hearing the distress call). We then fed novel feature vectors into the same model and tested whether the samples fell into the predicted classes. The model was able to successfully separate distress calls, hence suggesting that infants adjust their distress calls according to the urgency of their needs and their initial distance to the mother. We were also able to classify the mother's response to those distress calls, suggesting that mothers responded according to the urgency of their infants' needs. We discuss these findings in light of the evolution of vocal flexibility in a primitive vocal signal, shared by our closest living relative.

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## The Structure and Function of Female Chimpanzee Pant-Hoots

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The long-distance pant-hoot calls of chimpanzees have a compound structure, incorporating multiple elements and phases. Male pant-hoot calls have been studied widely and encode a range of information including caller identity, behaviour and group membership. Pant-hooting

in chorus has been shown to strengthen male social bonds, with potential impacts on individual fitness. However, almost nothing is known about female chimpanzees' production or use of pant-hoot vocalizations. We conducted a total of 473 h of focal individual follows on 30 female chimpanzees (*Pan troglodytes schweinfurthii*) in the Budongo Forest Reserve, Uganda. We collected data on all pant-hoots produced and received by the focal individual, together with information on their activity, oestrus status, and party composition. In addition, we opportunistically recorded 132 pant-hoots (70 female, 62 male) suitable for acoustic analysis. We describe the acoustic structure of female pant-hoots. A discriminant function analysis clearly distinguishes male from female pant-hoots; with variation in acoustic characteristics, such as number of elements in a phase, element length and element frequency, being greater between, as opposed to within, the sexes. We also investigate the use of female pant-hoots. We found no effect of oestrus stage within females on the rate of pant-hooting. Preliminary analyses show that the rate of pant-hooting varies depending on female parity, and on the sex and age class of dependent offspring. Females with only dependent daughters were more vocal than females with at least one son. Nulliparous females and females with infants of at least 4 years old were more vocal than those with infants of 3 years and younger. Our data offer new insights into the vocal behaviour of female chimpanzees and support the findings from male chimpanzees that pant-hooting behaviour varies with social context.

## The Specificities of Chimpanzee Vocalisations and Their Relationship to the Vocal Apparatus

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The production of vocalisations in non-human primates is often taken as an example in the quest for the understanding of the evolution of human language. Models have been made to look for the potential of monkeys' vocal tracts to produce speech-like sounds but meanwhile, the natural production of vocalisations in primates and especially apes, still remains poorly understood. It is generally admitted that the source-filter theory of human phonation also applies to most mammals. Essentially, the theory states that vocal signals are produced as a result of the independent contribution of the "source" (laryngeal structure producing the glottal waveform) and the "filter" (supralaryngeal vocal tract, shaping the glottal waveform into formants). This permits one to link the acoustic variation with the anatomy of the caller using the formula  $F_n = (2n-1)c/4L$ , which takes each formant separately. However, the first three formants can better be considered as generated by a two tubes model with the formant frequencies  $F_n$  defined by the equality  $A_2 \cotan(2\pi F_n L_1/c) = A_1 \tan(2\pi F_n L_2/c)$ , with  $L_1$  = back cavity length,  $L_2$  = front cavity length,  $A_1$  = back cavity area,  $A_2$  = front cavity area and  $c$  = 350 m/s. It is with this equation that we analysed some typical vocalisations of one of our closest living relatives, the chimpanzee. Data on wild chimpanzees, *Pan troglodytes schweinfurthii*, were collected in Budongo, Uganda. Nine adult males and ten adult females were followed and recorded. The chimpanzees' vocal repertoire presents both very harmonic and noisy vocalisations and very few formants. We calculated the 3 theoretical formants with the above equation from the measures of the vocal tract taken on the radiography of an adult female chimpanzee. We found formants mostly around high harmonics of the fundamental frequency. We discuss the possibility of the coupling between the source and the filter or the presence of another source (resulting from tension of the cartilaginous glottis) in the light of the chimpanzee's vocal apparatus, which, while being broadly similar to that of humans, also presents key differences.

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## On the Origin of Hemispheric Specialization for Language: Hand and Brain Asymmetries using MRI in Baboons (*Papio anubis*)

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Language is a unique system of communication in humans and involves hemispheric specialization and complex cortical organization of the brain. Given the phylogenetic proximity between humans and non-human primate species, a comparative approach to lateralization of the communicative system and to its cortical organization in apes and monkeys might enable the detection of the potential precursors of hemispheric specialization for language processing in our common ancestors. In previous studies we found that both chimpanzees and baboons – a non-hominid Old World monkey species – showed a robust predominance of right-hand use for communicative manual gestures specifically, indicating that the left-hemisphere might be dominant for the control of gestural communication. In the present brain studies using MRI at the Centre IRMF of Marseille, we investigate the anatomical brain asymmetries of some of the key cortical regions for language in 96 olive baboons (*Papio anubis*) which were housed in social groups at the Station de Primatologie CNRS. We found, for the first time in a non-hominid species, human-like significant neuroanatomical asymmetries toward the left hemisphere for the planum temporale surface and toward the right hemisphere for a specific portion of the Superior Temporal Sulcus's and of the Arcuate's depth. Interestingly, inter-hemispheric asymmetries of the central sulcus depth were shown to be significantly driven by the contralateral direction of handedness (i.e. left- or right-hand), which were previously assessed in these individuals using a bimanual coordinated task. These collective findings suggest that the continuity of hemispheric specialization between apes and humans extends to baboons for key structures of language and handedness. These findings argue that prerequisites of hemispheric specialization for language and handedness might date back to the common ancestor of Catarrhini at 30–40 million years ago.

## Oral Communications Health

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### Considering the Diversity of Human-Non-Human Primate Contacts for Disease Emergence

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Human-non-human primate contact is used as a proxy for risk assessment of pathogenic exposure; it is the basis for public health recommendations and non-human primate (NHP) conservation policies. Direct human contact with NHPs purportedly catalyzed the HIV pandemic and several Ebola outbreaks, and conversely, human pathogens pose a serious threat for endangered NHPs, especially great apes. Although “contact” is frequently used, it is employed incon-

sistently and imprecisely, overlooking the range of pathogens, their transmission routes and directions and the people, practices, ecologies, histories and political economies that shape them. We focus on human activity profiles in one village in southeastern Cameroon and relations between these activity profiles and contacts – ranging from indirect (sighting faeces, food remains, or footprints) to physical – with 9 NHP species inhabiting this area. Fifteen volunteers (7 women, 8 men) documented their daily activities in the forest and contacts with NHP species from April to July 2016. Our results show a diversity of human activity profiles, even at this fine scale, with a greater contribution of gathering than hunting to differentiate these profiles. Moreover, contacts with great apes are mainly indirect. Even if indirect contacts are likely less risky than physical ones, the higher frequency of indirect contacts with great apes shows the necessity of taking better stock of the diversity of human–NHP contacts to assess pathogenic risk for both humans and NHPs. Our study offers new insight for rethinking contact through the lens of One Health, evaluating the diverse range of interactions between NHPs and humans that may facilitate pathogenic transmission, not just hunting or butchering practices as the sole human activities that transmit infectious disease. Our fine-scaled approach therefore offers a more robust and precise evaluation of engagements that increase pathogenic risks for NHP and human health.

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### **High Prevalences and a Wide Genetic Diversity of Simian Retroviruses in Non-Human Primate Bushmeat in Rural Areas of the Democratic Republic of Congo**

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Like the majority of emerging infectious diseases, HIV and HTLV are of zoonotic origin. Here we assess the risk of cross-species transmissions of their simian counterparts, SIV and STLV, from non-human primates (NHP) to humans in the Democratic Republic of Congo (DRC). A total of 331 samples, derived from NHP bushmeat, were collected as dried blood spots (DBS,  $n = 283$ ) or as tissue samples ( $n = 36$ ) at remote forest sites mainly in northern and eastern DRC. SIV antibody prevalences in DBS were estimated with a novel high throughput immunoassay with antigens representing the actual known diversity of HIV/SIV lineages. Antibody-positive samples were confirmed by PCR and sequence analysis. Screening for STLV infection was done with universal primers in tax, and new strains were further characterized in LTR. SIV and STLV infection in tissue samples was done by PCR only. Overall, 5 and 15.4% of NHP bushmeat was infected with SIV and STLV, respectively. A new SIV lineage was identified in Allen's swamp monkey (*Allenopithecus nigroviridis*). Three new STLV-1 subtypes were identified in Allen's swamp monkey, blue monkeys (*Cercopithecus mitis*), red-tailed guenons (*Cercopithecus ascanius schmidt*) and agile mangabeys (*Cercocebus agilis*). SIV and STLV prevalences varied according to species and geographic region. Our study illustrates clearly, even on a small sample size from a limited number of geographic areas, that our knowledge of the genetic diversity and geographic distribution of simian retroviruses is still limited and that humans continue to be exposed to relatively high proportions of infected NHP bushmeat.

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## PCR Detection of *Entamoeba histolytica* in Captive, Semi-Captive and Wild Primates in the Amazon Region of Ecuador

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PCR is the most sensitive method of detection for *Entamoeba histolytica*. This species is one of the protozoa having medical importance. It causes diarrhoea and even death in primates. As a result, it is of major concern for wildlife refuges and public health. This study determines the prevalence of *Entamoeba histolytica* in 72 primates from the Ecuadorian Amazon region to assess its possible transmission between primates and non-human primates. Faecal samples were taken from habituated groups and identified individuals from February 2011 to August 2014. DNA extraction was performed using a commercial kit. *Entamoeba* spp. was confirmed by PCR ( $n = 51$ ). These positive samples were submitted to specific primers of *Entamoeba histolytica* variants. From those positive samples only 3 had the human variant of *Entamoeba histolytica*. This study confirms the presence of *Entamoeba histolytica* in non-human primates. These results are also a contribution to ex situ conservation and in situ conservation of Amazonian primates through public health.

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## Vaginal Cytology as a Non-Invasive Method to Follow the Oestrus Cycle in Two Species of Non-Human Primates: Crab-Eating Macaque (*Macaca fascicularis*) and Black Lemur (*Eulemur macaco*)

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Reproduction management of non-human primate (NHP) species can be challenging due to the diversity of species and the lack of data on anatomy and physiology but it is critical for some species. To enhance reproduction management in captivity different tools are developed and adapted for each species. This involves: evaluation of male and female fertility, monitoring females' cycle, artificial insemination and assisted reproductive technologies. To have a better understanding of the physiology of a species and be able to help reproduction when needed, the monitoring of the oestrus cycle is essential. Non-invasive methods are always preferred because physical restraint and manipulation of wild species are stressful. Non-invasive endocrinological methods can be used on faeces or urine but these methods usually require access to a specialized lab and do not enable the oestrus cycle to be followed in real time. Analysis of exfoliated vaginal epithelial cells is a simple and non-invasive method which is used as a daily routine in canine species but there is little information regarding NHPs. Vaginal swabs were obtained during a whole

oestrus cycle in 9 crab-eating macaques and 2 black lemurs. In the macaque female group, the variations in colouration and swelling of the sex skin were also followed and blood was regularly collected. Cells of the vaginal swabs were stained using the monochrome RAL 555® method and classified as basal, intermediate or superficial. At the beginning of the cycle, there were basal and intermediate cells which tended to disappear. Bacteria and neutrophils were present. Around mid-cycle, when ovulation is supposed to occur, there were only superficial cells, no bacteria or neutrophils. During the second part of the cycle, intermediate cells followed by basal cells reappeared. Efficiency of this method to define the precise moment of ovulation will be discussed in correlation with dosage of circulating hormones.

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## Study of the Prevalence of Cestodosis in Wildlife and Primates in the Centre de Primatologie of Strasbourg

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From 2009 to 2016, we observed cestod cysts in 4 non-human primates (NHPs) of 3 different species (*Macaca fascicularis*, *Macaca tonkeana*, *Eulemur macaco*) living in the Centre de Primatologie of Strasbourg (CdP). Some diagnoses were subsequent to clinical symptoms (abdominal mass, abdominal effusion or paraplegia) but one was only discovered at necropsy with no related ante-mortem symptoms. The cestod species concerned were *Echinococcus multilocularis* and *Taenia martis*. Local wild small carnivores in Alsace such as foxes and martens are common definitive hosts of these parasite species. It is known that NHPs can become accidental intermediary hosts after ingestion of items contaminated by carnivore faeces. The CdP topography enables contact between wild carnivores and NHPs living in outside enclosures, so some of the wild carnivores can get close to the fence and the smallest ones can get through the fence. The following analysis will focus on the outdoor housed NHPs. As infestation can be asymptomatic, cestod prevalence could be underestimated in NHPs. This study aims to determine the parasite prevalence in NHPs in relation to the presence of local carnivores and rodents. One hundred and thirty eight carnivore faeces were collected in the CdP and in the forest nearby. Twelve Muroidea carcasses were randomly found in the CdP. PCR analyzes showed the presence of *Echinococcus multilocularis* in 3 Muroidea tissues and 20 carnivore faeces, all positive samples were confirmed by ADN sequencing. Sera from 89 NHPs were submitted for Western Blot analysis and showed positive serology in 8 individuals, none of them presenting any symptoms. In conclusion, cestodes are commonly present in the surroundings of CdP and NHP infestation occurs. Strategies of prevention in outdoor housed NHPs will be discussed.

## Oral Communication

### Use of NHPs and Some Alternatives

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#### Non-Human Primates in Neuroscience Research: The Case Against Its Scientific Necessity

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Opposition to monkey (non-human primate, NHP) experiments is significant: just 17% of the UK public supports macaque research to benefit people. Yet, these experiments continue based on claims of minimal harm to NHPs and substantial human benefit. However, both claims are refuted by evidence. Neurophysiology experiments can be some of the most severe, typically involving implantation of recording devices into monkeys' skulls, harsh water deprivation regimes and immobilisation during procedures lasting several hours per day, and these experiments can be conducted for years. They can cause severe stress, adversely affecting welfare and data reliability. We have reviewed claims of benefit, specifically in neuroscience, and show: there is a default assumption of, rather than robust evidence for, human relevance and benefit; human relevance and essential contribution and necessity of NHP experiments are overstated; the contribution and capacity of non-animal methods are understated and underappreciated; and confounding issues, such as species differences and effects of stress and anaesthesia, are usually overlooked. This is the case in NHP research generally, but we have focussed (based on explicit claims by NHP researchers for the need for their work) on the development and interpretation of functional magnetic resonance imaging (fMRI), deep brain stimulation, the understanding of neural oscillations and memory, and investigation of control of movement and of vision/binocular rivalry. The harm-benefit balance is skewed by under- and over-estimation of harms and benefits respectively, and non-animal methods are key contributory approaches to progress. The increasing power of other methods, including advances in fMRI and invasive techniques such as electrocorticography and single-unit recordings, combined with poor human relevance of NHPs and harms associated with NHP use, renders NHP neuroscience unnecessary. Neuroscience would be more beneficial for humans if it were conducted with a human focus.

## Oral Communication

### Individual-Based Models and Social Behaviour

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#### Proximate Mechanisms Underlying Primates' Complex Social Networks: A Modelling and Comparative Approach

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The proximate mechanisms giving rise to reciprocation and interchange of social behaviours in primates have been extensively debated. Three mechanisms have been proposed: "calculated reciprocity," "emotional bookkeeping" and "symmetry-based reciprocity". Based on ex-



perimental and observational data, researchers appear to favour emotional bookkeeping. A different approach to study potential mechanisms underlying reciprocation and interchange is by means of individual-based computer models. Three models, identical regarding the rules for individuals' social interactions, suggest mechanisms resembling "symmetry-based reciprocity" and "emotional bookkeeping" as the basis of reciprocation and interchange. "GrooFiWorld" suggests proximity-based interactions; "FriendsWorld" suggests proximity-based interactions and preferential interactions; the "Reaper model" suggests preferential interactions alone. Because the three models reproduce reciprocation and interchange, it is difficult to tell which one, if any, more accurately represents the empirical data. To clarify this, here we used a social network approach. We collected data from six captive and eight wild/provisioned groups belonging to eight macaque species and did a social network analysis. Then, we simulated each group in each model, analyzed the emergent social networks, and quantitatively compared empirical and models' networks. Results show that the three models capture to some degree the features observed in social networks of macaques. However, no model seems better than the others at fitting the observed data. Further, modularity, average eigenvector centrality, and degree of network centralization were poorly fit by all models. Social interactions in the models thus may be more simplistic than in reality and may miss some mechanism(s), e.g. accounting for third-party relationships. We will, in the future, study whether implementing this or other mechanisms may improve the fit between models and the empirical data.

### 3

## Symposia

### Symposium

## Primate Cultures: Updates and New Trends

### Long-Tailed Macaques Tool Use – A Cultural Behaviour?

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The cultural influence in primate tool use is most convincingly demonstrated in observed diversity between populations at small geographic scales, where ecological and genetic diversity can be controlled for. Long-tailed macaques (*Macaca fascicularis*) have been known to use stone tools to forage for marine food items along the coast lines in Southern Thailand and Myanmar. Observations of natural behaviour combined with field experiments and archaeological investigations of artefacts recently painted a diverse picture of macaque tool repertoires amongst populations. Additionally, a novel discovery showed that wild macaques crack open oil palm nuts (*Elaeis guineensis*) on Yao Noi Island in Ao Phang-Nga National Park, Thailand. Oil palm nuts appeared only recently on this island, following human introduction of this plant into the monkey habitat in the early 2000s. Our research site on Yao Noi Island covers the diverse habitats of wild long-tailed macaques, ranging from an intertidal zone, a sandy beach, to the steep coastal forest. Within the forest we located an abandoned and overgrown oil palm plantation where palm trees still regularly produce fruits. In order to assess the availability and densities of raw tool material, tool numbers, natural anvils and oil palm trees, we placed 13 line transects (a total of

1,600 m) throughout the potential home range of the macaques and recorded hammerstone weight, dimensions and material within 1 m of either side of the transects, as well as used anvils. We found a high abundance of nut cracking sites indicating a significant consumption of oil palm nuts by wild long-tailed macaques. This novel tool behaviour implies a transfer of typical macaque lithic technology used for marine prey to successfully exploit the relatively new oil palm nuts. Exploiting new food sources within the existence of the behavioural repertoire testifies an ability to take advantage of rapid environmental changes, a general feature of wild macaques. Such a high level of behavioural plasticity indicates the potential for macaques to exhibit cultural tendencies as it has been suggested to lie at the base of cultural behaviour in animals.

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### Experimental Field Investigations of Cultural Capacities in the Tool-Using Bearded Capuchin (*Sapajus libidinosus*)

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Experimental studies of captive capuchin monkeys and wild observational data indicate they are “cultural”, yet direct experimental evidence of social learning in wild individuals is lacking. The populations of bearded capuchins (*Sapajus libidinosus*) inhabiting the caatinga of the Serra da Capivara National Park (SCNP), in Brazil, are ideal for acquiring such evidence as they possess the largest toolkit described for monkeys. We present social network analysis and several open-diffusion experiments, involving posing novel foraging tasks to two wild groups of capuchins. Using network-based diffusion analysis we find, across tasks, that observation from close range, versus a distance, better predicts learning by naïve individuals, indicating observational learning rather than local/stimulus enhancement. We thus empirically support the argument that inter-population variability of toolkits in wild bearded capuchins is underpinned by cultural behaviour patterns. In addition, we present evidence for various biases in the cultural transmission of information in this species and briefly discuss how these biases compare to those seen in other species, including humans. For example, grooming networks outside the experimental context robustly predicted the diffusion of a task’s solution, highlighting the importance of considering the role of social interaction networks, as well as association networks, in primate cultural transmission studies. We also find evidence for a bias towards observing the most successful individuals, moderated by sex. Finally, we discuss findings from a study using a cumulative problem solving task, indicating that the capuchins are able to use social information to switch flexibly to higher payoff behaviour, a requirement for cumulative cultural evolution. Understanding the social context of tool use in New World monkeys provides comparative insight, beyond great apes, regarding the cultural evolution of technology.

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### Early Hominin Cultures – Based on High Fidelity Transmission?

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Culture is often defined as behaviour (including products) influenced by social learning. This is what I call the “wide net” definition of culture: it allows the study of culture across the animal kingdom (where it is indeed frequently found). But human behaviour is not only *influ-*

enced by social learning; it often fully *depends* on social learning: no animal species dances to arbitrary dance steps, has language, or builds social and physical tools that could not be reinvented on the spot by naïve subjects. I therefore call these cultural dependent traits (CDT). I will argue that CDT require special types of social learning, namely high fidelity transmission (e.g. Tango dance). They require these not only to stay afloat, but also to come about at all. I will further argue that modern non-human great apes (henceforth apes) are likely unwilling or unable to spontaneously show high fidelity transmission. While we clearly do see cultural traits in apes, this is fully to be expected given how wide a net the current cultural definition covers. A lack of high fidelity transmission however would mean that – outside human influence – apes could not support cultural *dependent* traits. One prediction that follows from this view is that ape cultural traits therefore should be re-inventible on the spot by apes naïve to the particular cultural trait (at least when they do not yet have another solution that works and when motivated; such evidence is indeed currently mounting). Early hominins might also have been unable or unwilling to engage in high fidelity transmission, which would have forced them to constantly ‘reinvent the wheel’ (i.e. the respective stone tools they made). And so, not only does this explanation follow from cognitive cladistics, but it would also explain the levels of stasis seen in early hominin tool use (a stasis across time, space and hominin species!). High fidelity transmission would therefore not only be rare today, it would also be an evolutionary late phenomenon.

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## Learning from the Immigrants: Dispersing Orangutan Males as Cultural Vectors

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Observational forms of learning have been shown in great apes and several other primate species in captivity. However, details of social learning pathways in the wild are rarely documented. In a previous study it has been shown that wild immature orangutans learn from experienced role models through peering (close range observing of another subject’s activities). However, the use of peering for cultural transmission of behaviour between members of the philopatric and the dispersing sex is not yet understood. In this study on a Bornean orangutan population (*Pongo pygmaeus wurmbii*) we examined whether dispersing males (so-called “unflanged males”), ranging outside their natal area act as cultural vectors for local individuals. Therefore 561 peering events were recorded during focal follows over a time period of 5.2 years. Our results were in line with the assumption that individuals socially acquire skills and knowledge through peering. We found that, overall, peering frequency decreased with a subject’s age. Infants peered mostly at their mothers, whereas juveniles showed a clear preference for peering at unflanged males, especially in the nesting and social context. In addition, individuals peered more at an unflanged male when feeding on rare food items, rather than on common ones. On top of peering for information, unflanged males may have also used peering as a social tool to promote tolerant associations with adult females and their offspring. The results suggest that unflanged males may function as cultural vectors for the local population and indicate how innovations could be transferred between and within orangutan populations.

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## Combining Field Experiments and Long-Term Field Data: Two Examples to Understand Culture in Wild Eastern Chimpanzees (*Pan troglodytes schweinfurthii*)

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Current research on animal culture has a strong focus on the social learning mechanisms that sustain the spread of socially transmitted behaviours but less is known about the persistence of cultural behaviour following innovation in wild groups. Additionally, ecological variation has been shown to influence the appearance and maintenance of tool use in animals, either due to necessity or opportunity, but little is known about the relative importance of these factors. Here, I want to address both questions, underlining how the combination of observational and experimental data collected in the Sonso chimpanzee community of Budongo Forest, Uganda (*Pan troglodytes schweinfurthii*) leads to powerful analyses associating the strengths of the two approaches. On the one hand, over the last nine years, over 50 subjects interacted with natural logs, which contained a variety of substances, from energetically valuable honey to boiled rain water (honey-trap and water-trap experiment, respectively), which were accessible only through tool use. Engagement with the honey-trap was highest after periods of low fruit availability involving more travel between food patches, while instances of actual tool-using were significantly influenced by prior travel effort only, although no novel tool use was developed. On the other hand, the Sonso chimpanzees naturally developed a novel behaviour in 2011, which we identified as moss-sponging: using moss instead of leaves to manufacture sponges. While the behaviour initially spread through proximity-based networks, subsequent analyses combining field experiments and association patterns between individuals since the emergence of the behaviour showed that moss-sponging has spread mainly through matriline. Combining observational data with experimental results may constitute an important way to test theoretical hypotheses on culture to inform discussions on primate behaviour and human evolution.

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## Discovering the Base of the Iceberg: A New Way to Look at Cultural Repertoires in Primates

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Biologically, culture is defined as innovations that are spread and maintained between and within generations by social learning. The most commonly used way to detect animal culture is the method of exclusion which infers cultural processes if a behaviour is common at some sites but is absent at others, while ruling out ecological and genetic explanations. However, this method ignores any behavioural variant with ecological or genetic correlates, even if the behaviour is in fact socially transmitted. We suggest a new way to measure the size of cultural repertoires by directly looking at evidence for social learning. We compared cultural repertoires of a population of Sumatran orangutans (*Pongo abelii*) at Suaq to a population of Bornean orangutans (*Pongo pygmaeus wurmbii*) at Tuanan, applying the method of exclusion as well as counting socially transmitted skills and knowledge using our long-term data bases. To detect social learning we looked at patterns of peering (attentive close range watching). We found that social learning was significantly more common at Suaq, the population previously shown to be more sociable. Accordingly, repertoires at Suaq were larger and also more complex (of higher processing intensity) than the ones at Tuanan. Also, in both populations, the repertoires captured by the method of exclusion

were a substantially smaller subset of the ones detected by counting the number of socially learned skills. The culturally transmitted behaviours which were not captured by the method of exclusion were socially transmitted behaviours that were present at both sites or showed ecological correlates. Our results show that whereas the method of exclusion is a conservative way to detect the presence of cultural processes, to estimate and compare actual repertoire sizes one needs to look at direct evidence of social learning. Furthermore, not all social learning leads to between-population differences and many cultural variants may be influenced by ecological conditions.

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## Primate Behavioural Flexibility in the Anthropocene

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Humans and their activities are major agents in transforming habitats. For non-human primates, managing the risks and opportunities presented by human proximity and fast-paced landscape modifications sets the context for novel selection pressures. In large-brained and long-lived species, this demands cognitive and behavioural flexibility which allows rapid and reversible responses to changes in environmental conditions. Using chimpanzees (*Pan troglodytes verus*) inhabiting a forest-farm mosaic at Bossou in Guinea as a case study, we show how individuals are modifying their behaviour through: (1) patterns of human crop selection, (2) use of tools to access novel resources, including fermented raffia palm sap, and (3) changes in grouping patterns and “division of roles” in response to anthropogenic risk. We are only just starting to understand how anthropogenic factors drive new patterns of behaviour in non-human great apes and other primates, and the limits of primate flexibility in a changing world. We discuss an evolutionary and cognitive framework for future research direction suggesting that shared human-impacted mosaic landscapes offer contemporary models for palaeoanthropological reconstructions of how our early ancestors might have overcome novel risks during periods of environmental variability, as well as opportunities to use a quasi-experimental approach to examine ape behaviour and cognition the wild.

## Symposium

### Primates at the Edge: Mechanisms and Consequences of Raiding

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## Towards a Historical Ecology of Chimpanzee and Baboon Crop-Foraging: Case Studies from Senegal (c. 1900) and Guinea (1920–1950)

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Present-day discourse on the ecological causes of primate crop-foraging is inspired by a dualistic perspective on nature-society relationships rooted in Malthusian views: its probability is said to increase as human populations grow, progressively expand into forests and convert forests

to agricultural land, thereby bringing humans and animals into more direct competition over food resources, finally forcing primates out of their natural habitat into fields. We will discuss the validity of this narrative, which informs contemporary conservation policies, using late 19th century travel accounts and archival sources from colonial forestry administrations as well as from Guinea's former Pasteur Institute. This will allow us to account for past events of chimpanzee and baboon crop-foraging in southeast Senegal (c. 1900) and in various regions of Guinea (1920–1950). It appears that: (1) crop-feeding events reported in the literature are perhaps as much an artefact of recent attention paid to the phenomenon as of a consequence of an actual rise in crop-raiding; (2) baboon crop-feeding was more frequent than that of chimpanzees in the past; (3) we could be facing a phenomenon of baboon population expansion rather than human encroachment into “heir” habitat, related to the near-disappearance of their predators (lions and leopards) following the 19th century West African trade. Overall, the assumption that crop-foraging did not exist before, or was infrequent in the past, needs to be revised, considering both the history of agricultural practices and of animal population dynamics. This evidence pleads for the building of empirical and more complex historical models of crop-raiding that can lead us to a better understanding of current trends.

### **Behaviours Used by Olive Baboons to Raid Food on an Asphalted Road Crossing Sebitoli Area, Kibale National Park, Uganda**

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Throughout sub-Saharan Africa, baboons are often reported to perform raids on anthropogenic food, either in fields and gardens (i.e. crop-raiding) or inside urbanized or touristic areas. At several locations, raids occur on roads that run through the home range of baboons. Interestingly, “road-raiding” requires direct interactions between human and non-human primates: baboons have to request food from people because food is usually kept inside vehicles. Over the summer of 2016, we started to monitor olive baboons (*Papio anubis*) regularly observed to feed on anthropogenic food remains (fruits, snacks, left-overs from road-side fast-foods, and even liquids) on an asphalted road crossing Sebitoli area, in the northern part of Kibale National Park, Uganda, using scan and focal animal sampling methods. From mid-July to mid-September, we video-recorded 168 events of road-raiding, i.e. sudden assault directed towards people in vehicles, from a group of 13 baboons (1 adult male, 6 adult females, 1 sub-adult male, 1 sub-adult female, 4 infants) that were already habituated to humans. Those baboons mainly started road-raids by walking slowly in front of oncoming vehicles and climbing onto them (front, windows or back). Males interacted more often with people travelling inside vehicles than females. However, females were also involved in road-raiding as they fed on food items remaining on the road. No other baboon group was observed feeding on anthropogenic food on the same road, although a group of up to 23 individuals was regularly observed feeding on herbaceous vegetation and trees close to the road. This pilot study indicates that road-raiding is not performed equally by all the individual baboons in the monitored group, which is of interest for understanding the mechanisms and consequences of this behavioural practice on the health, social structure, range use and time-activity budget of the baboons. This also highlights the importance of informing people about the risks of feeding the monkeys (e.g. monkey aggression, pathogen transmission, traffic jams and accidents).

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## Response Facilitation in the Robbing and Bartering Activities of Balinese Long-Tailed Macaques

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Primates living in highly anthropogenic habitats such as tourist temple sites are required to have flexible and innovative foraging strategies. To do so, they can use social information and directly learn by observing group members. We investigated the role of response facilitation as a direct social influence mechanism underlying the expression of robbing and bartering (RB) by free-ranging Balinese long-tailed macaques (*Macaca fascicularis*) at Uluwatu Temple (Indonesia). RB consists of stealing inedible objects from visitors (e.g. glasses) and exchanging them for food with humans. We video-recorded all occurrences of spontaneous RB events between September 2015 and August 2016, and collected 15-min focal samples on neighbour individuals (NF) immediately after they watched a RB event. We also collected matched-control focal samples (MCF) on the same witnesses located at similar distance to former demonstrators, in the absence of any RB events. The RB practice was customary in the Uluwatu population: 55.4% of all able-bodied individuals robbed and 40.9% could also barter. Our results support the role of response facilitation: watching RB performed by conspecifics temporarily increased the probability of the witness engaging in RB on its own. Macaques robbed/bartered more often and within a shorter time window ( $n = 115$  NF/MCF dyads,  $p < 0.001$ ) after watching group members engaging in RB than in control conditions (RB by focal occurred in 70% of NFs versus 21% in MCFs). The social influence occurred mainly during the first minutes after watching RB, after which RB frequency returned to baseline. By demonstrating social influence on the expression of RB, our results support the cultural nature of the RB practice at Uluwatu. Supported by the “Discovery Grant from the Natural Sciences and Engineering Research Council of Canada.”

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## Chimpanzee Crop-Foraging Preferences and Perception of Risk in a Human-Dominated Landscape, Uganda

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Anthropogenic habitats can provide primates with new food sources, but entering agricultural areas also presents risks to primates through confrontations with local people. Primates will forage in cultivated areas based on multiple factors, including crop availability, wild food availability, and the degree of risk associated with obtaining the desired crop. We assessed chimpanzee (*Pan troglodytes schweinfurthii*) feeding preferences and risk perception when foraging on mangoes, a subsistence crop, and commercially-grown sugarcane at Kasongore, Uganda. To avoid following chimpanzees into crop gardens, mango trees were monitored for feeding traces daily during the peak fruiting season (May–July 2016). Sugarcane consumption was recorded using direct observation over the whole study period (August 2015–July 2016). Chimpanzees at Kasongore ate crops habitually, almost on a daily basis. Guarding presence and terrestrial vegetation cover were the most important factors determining chimpanzee mango foraging choices. Chim-



panzees targeted sugarcane year-round regardless of wild food availability. Chimpanzees showed preferences for particular mango and sugarcane varieties of both crops, implying taste may play a role in foraging choices. To reduce risk associated with crop-foraging, chimpanzees fed in large parties and remained quiet to avoid detection. Lone females joined male parties or sporadically formed large all-female parties. Despite chimpanzees at Kasongoire exhibiting a level of risk aversion, they forage heavily on crops. As in similar human-dominated sites, mangos are an integrated part of their diet at Kasongoire, while sugarcane feeding by chimpanzees has not previously been recorded at the habitual level observed in this study. An improved understanding of chimpanzee risk perception in anthropogenic habitats can help develop strategies to reduce the impact of crop-foraging on local livelihoods.

## Food despite Danger: Assessing the Mechanisms of Crop-Raiding in Baboons

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Transformation and loss of natural habitat from urbanisation and agriculture provides new opportunities for primates, especially baboons, to feed on anthropogenic food sources. Currently, mitigation strategies fail to target the individuals responsible for initiating and maintaining the raiding behaviour. As primates mainly raid crops in groups, we use our knowledge about collective movements in the wild (i.e. when a group of animals move together in the same direction thus resulting in a change of location) to investigate crop-raiding behaviour of a group of 40 chacma baboons (*Papio hamadryas ursinus*) in Zimbabwe. We recorded baboon movement and behaviour with a camcorder. Most crop-raiding events involved less than 20% of the troop and lasted less than 3 minutes, preventing raiders being detected by farmers. Our results suggest a high synchronization of raiders and that raiding was based on a collective decision similar to movements in natural environments. Although raiding parties were composed of all sex and age categories, adult females and, even more frequently, adult males mainly initiated raids and made preferentially direct raids (without stopping on the road). These frequent initiators might have greater energetic needs or be more risk-prone. Indeed, when raiding crops, animals can be caught or killed by farmers. To investigate why adult males initiated raids more frequently, we quantified the attitude towards risk of 10 adult male olive baboons (*Papio hamadryas anubis*, a species of similar ecology to chacma baboons, and one which also raids crops) in a food context, where a human experimenter simulated the danger. This complementary experiment – conducted in controlled conditions in Rousset (France) – mimics the risk that a baboon takes when raiding in a field guarded by a farmer. The results revealed that baboons are risk-averse. Nevertheless, they adapt their behaviour according to the human presence and the amount of the reward. We tested if differences between individuals could be related to age, weight or temperament and found that those differences could be explained by impatience (temperament) and weight. Further studies need to be conducted in order to identify factors underlying a risk proneness attitude in a crop-raiding context.

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## Sex Differences, Seasonality, and Macronutrient Balancing in the Diet of Chimpanzees Inhabiting a Forest-Agricultural Mosaic

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Many primates face spatial and temporal fluctuations in food availability, which can significantly affect their ability to meet nutritional requirements. Anthropogenic disturbances and influences, such as agriculture, human presence and infrastructures, can further impact seasonal food availability, dietary composition and nutrition. Primates residing in anthropogenic landscapes often incorporate cultivars into their diets. However, the nutritional drivers behind cultivar consumption are poorly understood. We examined variations in chimpanzee (*Pan troglodytes verus*) macronutrient intake from wild and cultivated foods between sexes and seasons over a 1 year period in Bossou, Guinea. We used the geometric framework of nutrition to examine proportional contributions of macronutrients to the diet and nutrient balancing. We conducted continuous focal observations of adult individuals ( $n = 10$ ) to record all feeding bouts and conducted nutritional analyses of plant foods (25 wild species; 11 cultivated species). We found no sex differences in chimpanzees for wild or cultivated food or macronutrient intakes; however, females showed higher intakes of total food (i.e. wild and cultivated combined), digestible fibre (NDF), and protein when controlling for metabolic body mass. There were no differences in wild or cultivated food intake between seasons; however, lipid and protein intake from cultivars were higher when wild fruit availability was low. Chimpanzees maintained a constant proportional intake of protein while allowing carbohydrates and lipid intakes to vary. Furthermore, they were able to maintain a consistent balance of protein to non-protein (carbohydrates, lipids, and NDF) energy across the year. Our results suggest that Bossou chimpanzees suffered little seasonal constraints in food quality or availability since they were able to combine their consumption of available wild and cultivated foods to achieve a balanced diet. These findings contribute significantly to our understanding of primate nutritional requirements and their ability to meet these in disturbed environments.

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## Pesticide Exposure and Facial Dysplasia in Wild Chimpanzees and Baboons in Sebitoli (Kibale National Park, Uganda)

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Prenatal exposure to pesticides can affect foetal development and induce irreversible abnormalities in humans and animals. Wildlife in Sebitoli area in the northern part of Kibale National Park in Uganda must cope with proximity to human activities including industrial tea plantations. In addition, the chimpanzees (*Pan troglodytes schweinfurthii*) and baboons (*Papio anubis*)

regularly feed on maize and plantain in neighbouring gardens. A large proportion (25%) of the 66 chimpanzees monitored since 2008 by the Sebitoli Chimpanzee Project exhibit facial abnormalities (reduced nostrils, cleft lip), limb deformities, reproductive problems and hypopigmentation. In addition, 17% of a baboon troop have similar severe nasal deformities. These pathologies could have a congenital component, potentially exacerbated by environmental factors. Chemical analyses – consisting of extraction, clean-up and chromatography (gas [GC] or high performance liquid [HPLC] chromatography) – of samples collected from 2014 to 2016 showed that mean levels of pesticides in fresh maize stems and seeds, soils, river sediments and fish in the vicinity of the chimpanzee territory exceed recommended limits. As certain of these pesticides are thyroid hormone disruptors, we postulate that excessive pesticide use in the Sebitoli area may contribute to facial dysplasia in chimpanzees and baboons through this endocrine pathway. Chimpanzees are endangered primates and considering environmental pollution as a threat to their survival is a matter of urgency.

## Symposium

### What Can an Interdisciplinary Approach Tell Us about the Evolution of Grasping and Manipulation?

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#### Introduction: The Necessity to Develop an Interdisciplinary Approach to Understand Grasping and Manipulation

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Grasping and manipulation are widespread among primates and are associated with pronounced morphological, dietary, social and locomotor variation, prompting several questions. Is the origin and evolution of grasping in primates derived from necessities associated primarily with feeding or with locomotion and other social behaviours? Are there grasping abilities that are unique to humans? What is the variability in grasping abilities among primates? This symposium presents an overview of grasping and manipulation in primates. To do so, contributors explore the interaction between primates' upper limb anatomy, functional morphology, ontogeny and biomechanics, and how they perform diverse functions from locomotion to manipulation. This symposium will show the need to develop integrative studies to understand grasping and manipulation functions as well as their evolutionary mechanisms and how this can help infer the abilities of fossil specimens.

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## The Evolution of Hand-Grasping Behaviours among Strepsirrhines

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Most studies addressing evolutionary questions on grasping abilities have focused on great apes and have shown that they display a high variety of grip types, including some patterns originally thought to be human-specific. However, the evolutionary mechanisms underlying fine grasping abilities remain misunderstood. Strepsirrhines are a monophyletic group of primates, including roughly 60 highly ecologically, morphologically, and socially divergent species, making them excellent models to understand better the ecological and social factors driving the evolution of grasping ability. The present study aimed to quantitatively determine the different behavioural strategies adopted by different strepsirrhine species when grasping immobile food items in order to discuss the links between ecological or social factors and hand-grasping in an evolutionary context. We collected data for 86 individuals of 22 different species belonging to six of the seven strepsirrhine families, excluding Lepilemuridae. We videotaped each individual in its home enclosure during its normal feeding periods. We annotated a total of 5,472 grips ( $64 \pm 4$  grips per individual) characterised by the body part(s) involved as oral, unimanual, bimanual, combined oral-unimanual, or oral-bimanual. The two main grip types used were mouth (74–43%) and unimanual (44–24%) grips, but grasping strategy was affected by food properties. MANOVAs performed on the transformed proportion of the different grip types indicated significant effects of arboreality level, diet, locomotion and infant carrying pattern while grasping big items, and significant effects of arboreality level and diet while grasping small items. The presence of a phylogenetic signal suggested that closely related species have more similar behavioural patterns. When considering phylogeny, only the effect of the arboreality level remained significant for both big and small items.

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## Super Grip Strength Performance in a Small Primate (*Microcebus murinus*): Influence of Morphology, Environmental Context and Genes

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Grip strength is particularly important for arboreal species, which rely on this physical ability to grab and hold branches. However, the factors determining inter-individual variability in performance can be numerous, including the individual's early life parameters (birth weight, growth rate), current determinants (body dimensions, age and sex) and inherited genes. To explore the determinants of grip strength, we asked (1) whether this physical performance is influenced by morphology, age, sex, and the environment experienced early in life and (2) how this trait is genetically transmitted. We studied a captive colony of grey mouse lemurs (*Microcebus murinus*), in which animals are monitored from birth to death, to analyze grip strength via direct measurement of physical force with a grip test. As an arboreal primate, grip strength is crucial for its survival. But also once a year, male grey mouse lemurs need to monopolize a female by grabbing her during the 24 h of female ovulation. We collected data on forelimb dimensions and pull strength of 400 individuals with known maternal identity and with information on birth weight,

weight at three months and litter composition. We performed heritability estimations using the animal model to account for the effect of genes in the adult phenotype. Grip strength in this species allows individuals to pull 10 times their own weight and is not directly influenced by early life parameters, but is impacted by body weight, size and age. Larger body sizes are positively correlated with higher grip strength and body size is positively influenced by birth weight and growth rate. When corrected by age and body weight, grip strength is heritable at 11%. This shows that grip strength is mostly influenced by an individual's current determinants, early life environment and genes, suggesting that grip strength is under several evolutionary constraints. However, the direct impact on fitness still needs to be tested.

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## **Ontogeny Recapitulates Phylogeny: The Ontogeny of Manipulation Complexity within 31 Primate Species**

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A major characteristic of primates is their ability to perform a variety of food manipulations with their hands. These manipulative skills vary greatly in complexity between different species. However, it is not known in which order particular food manipulations emerge during ontogeny and whether this order is consistent across species. In this study, we assess whether the interspecific order of the complexity scale assigned in a previous study of adults in 37 primate species matches the intraspecific order of emergence of these manipulation categories during ontogeny. We examined longitudinal skill development from over 10,000 food manipulation bouts in 143 individuals of 31 primate species at 13 different European zoos. We started to observe immatures during the first week after birth and continued behavioural sampling at regular intervals until individuals achieved adult-level skill competence. Although individual and species variation in the timing of appearance and frequency of use of different manipulative skills were substantial, almost all observed individuals (97.7%) followed the same ontogenetic sequence, suggesting that the order of emergence of manipulative skills during development is conserved. Primates developed from single to multiple-object handling, from unimanual to bimanual manipulations and from synchronised to asynchronised finger and hand movements. This order of emergence of manipulative skills during ontogeny followed exactly the interspecific order of the complexity scale. Thus, the ontogeny of manipulation complexity seems to recapitulate its phylogeny.

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## **Comparison of Hand Use and Forelimb Mechanics of Vertical Climbing in Wild Mountain Gorillas and Free-Ranging Chimpanzees**

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Biomechanical analyses of great ape arboreal locomotion in a natural environment are scarce, thus limiting attempts to correlate behavioural and habitat differences with variation in skeletal morphology. However, little is known about arboreal grips and hand postures, or how

these might vary with forelimb posture during vertical climbing on natural substrates of different sizes. The aim of this study was to compare temporal kinematics of hand and forelimb use during vertical climbing in wild, habituated mountain gorillas (*Gorilla beringei beringei*) of the Bwindi Impenetrable National Park (Uganda) and sanctuary chimpanzees (*Pan troglodytes*) of the Chimfunshi Wildlife Orphanage Trust (Zambia) to assess differences in climbing styles that may relate to variation in hand or forelimb morphology and body mass. We investigated hand and forelimb posture coupled with temporal gait parameters during vertical climbing (both ascent and descent) in 15 mountain gorillas and 8 chimpanzees, using video records ad libitum. In both apes, forelimb posture was correlated with substrate size during both ascent and descent climbing. Both apes used power grips and a diagonal power grip, involving 3 different thumb postures. Gorillas showed greater ulnar deviation of the wrist during climbing than chimpanzees, and the thumb played an important supportive role when vertically descending compliant substrates in gorillas. Comparisons of temporal gait parameters indicated that large-bodied gorillas exhibited significant longer cycle duration, lower stride frequency and generally a higher duty factor than chimpanzees. This study revealed that wild mountain gorillas adapt their climbing strategy to accommodate their large body mass in a similar manner to that found in captive western lowland gorillas, but that the sanctuary chimpanzees showed less variation in their climbing strategy within a natural environment than has been documented in captive bonobos.

## **The Role of Prehensile Hands and Feet of Cotton-Top Tamarins during Climbing on Obliquely Oriented Supports**

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Successful exploitation of the terminal branch habitat is regarded as a key to early primate evolution. When foraging in this habitat, mammals constantly encounter flexible branches that bend under the animals' weight and form steeply inclined supports. Being able to grasp thin supports is therefore important and, not surprisingly, independently evolved several times in fine branch specialists. It has previously been shown that during locomotion on horizontal branches the forelimbs have a net-braking role, whereas the hind limbs adopt a net-propulsive role. Our study focus on how cotton-top tamarins (*Saguinus oedipus*, Callitrichidae, Primates), which have previously been proposed as modern analogues for a hypothetical stage in early primate evolution, meet the specific functional demands of navigating thin, branch-like supports of different orientation. In vivo x-ray motion analysis of three tamarins was combined with synchronous single limb substrate reaction force measurements to discern limb mechanical adjustments to support orientation. Generally, our results can be interpreted to reflect an emphasis of the functional roles of the forelimbs (net-braking) on declines and of the hind limbs (net-propulsive) on inclines. On the steepest inclines, tensile forces were exerted by the hands, whereas on the steepest declines, tensile forces were exerted by the feet. This biomechanical evidence sheds light on the adaptive significance of hand and foot prehensility in the complex, three-dimensional small branch habitat. The study demonstrates how the combination of prehensile hands and feet may have enhanced the exploitation of the small branch habitat during early primate evolution.

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## Form and Function of the Hominids Thumb: Link between In-Hand Movements and the Trapeziometacarpal Complex

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It is traditionally considered that humans possess more complex manual abilities than non-human primates, which is often explained by human-specific morphological features, including a long, mobile and powerful thumb. However, the actual manual abilities of primates have yet to be fully explored, as does their hand morphology. Therefore, we need to better understand the real manipulative abilities in extant primates by investigating their hand anatomy and function. The aim of the present study is to link both the in-hand movements (i.e. finger movements involving tool movement in the hand) used by humans and the other great apes during an identical complex tool-use task, and the overall morphology of their trapeziometacarpal complex (i.e. the trapezium and the first metacarpal). The frequency and the kind of in-hand movements were quantified frame by frame by video analyses during the maze task (recovery, with a tool, of walnuts positioned on a wooden maze). We classified in-hand movements in two categories; simple movements involving one finger or two fingers moving in opposite directions simultaneously, and complex movements involving sequential grasp and regrasp of the tool with independent co-ordination of fingers. The overall shape variability of the trapeziometacarpal complex was quantified using a 3D surface geometric morphometrics approach. A multivariate analysis of shape variation of the trapezium clearly distinguished *Homo* from great apes. The analysis of the first metacarpal distinguished *Homo* from *Pan* and *Pongo*. Shape variability seemed to be linked with the in-hand movements used in the same frequency by humans and African great apes but not by orangutans. Moreover, humans used simple and complex movements whereas African great apes used only simple movements. The different shapes of the trapeziometacarpal complex between hominids are certainly constrained or favored by factors such as locomotor behaviour and manipulative abilities.

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## Form and Function of the Bonobo Hand

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In the course of human evolution, hominins have acquired an unsurpassed manual dexterity. This unique dexterity is associated with morphological adaptations in the hand, and in particular in the thumb. Modern humans have a relatively long and robust thumb and a saddle-shaped basal thumb joint or trapeziometacarpal joint. This particular configuration allows high mobility (e.g. full opposability) as well as forceful precision and power gripping which is required for tool manufacture and use. Recent field observations have also documented tool-use in bonobos, despite their relatively short and gracile thumb. Detailed anatomical information of the bonobo hand and thumb is, however, largely lacking or inferred from chimpanzee anatomy. The aim of our study was to quantify the anatomy of the bonobo hand and to investigate the relation with its functional capacities. We performed detailed dissections of a series of unembalmed bonobo forearms and hands to quantify the hand musculature. Cadavers were obtained from different European zoos from animals that died under natural circumstances. Muscle parameters were obtained from all extrinsic ( $n = 5$ ) and intrinsic ( $n = 7$ ) hand muscles (e.g. muscle-tendon unit length, muscle mass, physiological cross-sectional area). In addition, CT and microCT scans were



obtained of each specimen to quantify the three-dimensional geometry and internal bone parameters of the first metacarpal and trapezium. The results indicate that bonobos display a high inter-individual variation in muscle size and configuration. Moreover, the size and functional capacity of the muscular envelope of the bonobo thumb is very similar to the human configuration. This could explain the high dexterity and tool use observed in free-ranging bonobos. Using our integrated approach, we obtained a complete and unique anatomical dataset of the bonobo hand and thumb which will be used in a next step to create a three-dimensional musculoskeletal model of the bonobo hand.

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## **Coevolution between Grasping Ability and Forelimb Shape in Strepsirrhines and Platyrrhines**

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Fine prehensile activities are thought to be uniquely associated with the evolution of human hands and with tool-making and tool-use in the earliest humans. However, there is no holistic approach establishing the link between the morphology of the forelimb and grasping ability in living primates. The present study aims to understand the relationships between grasping behaviour and the morphology of forelimb in a phylogenetic framework in strepsirrhines and platyrrhines. On one hand, we analyzed behavioural data on food prehension (grasping with the mouth, one hand, two hands, the mouth and one hand, the mouth and two hands) for 92 individuals belonging to 22 species of strepsirrhines and 30 individuals belonging to 11 species of platyrrhines. On the other hand, we performed geometric morphometric approaches on the long bones of the forelimb obtained from collection specimens. Thus, we evaluate the strength of the co-variation between grasping behaviour and forelimb bone shape in primates. The data obtained show a phylogenetic signal in forelimb morphology in primates in relation to grasping and manipulation behaviour. Our results indicate that there is a co-evolution between grasping behaviour and the shape of the humerus and radius. Interestingly, strong differences in grasping behaviour and forelimb shape are observed between nocturnal and diurnal species of strepsirrhines.

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## **Forelimb Musculature, Arboreal Locomotion and Substrate Use in Primates**

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Life in a 3D arboreal environment implies that the locomotor performance of the animal is challenged by the discontinuous nature and complexity of the arboreal substrates. Arboreal locomotion, thus, imposes selective pressures that may affect the anatomy of the appendicular skeleton as the limbs have to be mobile to reach across discontinuities yet at the same time need to be able to generate a firm grip. Particularly in primates, the evolution of arboreal locomotion and grasping behaviour are tightly linked. Moreover, primates exhibit a variety of locomotor modes

and grasping abilities. The present project aims at better understanding the relation between quantitative muscle anatomy of the forelimb and locomotor mode. The forelimbs of strepsirrhine primates were dissected, muscle mass and fibre length were obtained and physiological cross-sectional area was calculated in order to describe the functional properties of the forelimb musculature. In accordance with a previous case study on carnivores, arboreal primates are expected to show a greater force-generating capacity of the forelimb flexor and retractor muscles as well as a larger excursion capability of the adductor muscles. In addition, the relation between quantitative muscle anatomy and grasping ability in the context of arboreal locomotion will be analysed. We expect that taxa grasping relatively small branches more frequently differ from taxa grasping relatively large branches in having extensor muscles that allow for more stretch (longer fibres) and stronger flexors. Ultimately, the comparison of the functional link between limb structure, locomotion mechanics and associated grasping abilities will shed light on the muscular adaptations of the forelimb associated with an arboreal lifestyle. This provides a good basis for future studies investigating the relation between quantitative muscle anatomy and grasping behaviour in non-locomotor roles such as feeding.

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## **Power Grip or Precision Handling?**

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A review of the relevant literature, my own research and that of my former co-workers show that the hands of primates are organs used for locomotion as well as for precise manipulation. The overall shapes of primate hands commonly fit precisely to the mechanical needs of efficient and energy-saving locomotion, and, in some “lower” species, to ideomotoric tasks as well. The mechanical stresses acting within the hand commonly reach their greatest values in locomotion, simply because the full weight of the animal, or even more (during rapid movement), is regularly transmitted through the hand to a substrate. For survival, it is obviously essential that these stresses can be sustained by the anatomical structures of the hand without danger of failure. Minimal weight, combined with maximal strength is obviously advantageous. For fulfilling both requirements, hands need a specifically defined morphology. Likewise, the proportions of the hand directly influence the mode and energetic efficiency of locomotion. By contrast, most manipulations, especially those summarized under “precision grip” do not imply, nor require the input of great forces. Therefore, morphological specialisations of the hand cannot be expected if they are in conflict with the above mentioned necessities of locomotion. Observations have shown that many primate species develop specific methods of precision handling, depending on their existing hand shapes. In the case of a particular manipulation, such as the use of heavy tools, that requires exceptional force input, the hands are loaded as in locomotion. The efficiency of precision handling in primates depends on absolute size, and its variability and importance are commonly under-estimated.

## Symposium

### Sociality and Health in Primates

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#### Urinary Neopterin Increases during a Respiratory Outbreak in Wild Chimpanzees (Taï National Park, Côte d'Ivoire)

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Life history models predict tradeoffs in energy allocation between balancing health and reproduction, with increasing evidence suggesting that individual health is key in mediating links between sociality and fitness. To estimate variation in individual health, measuring immune response throughout an animal's lifetime can provide valuable insights on costs of immune activation in the context of behavioural ecology. While traditional methods assessing general health were mainly invasive, recent methodological advancements have found promising biomarkers utilizing non-invasive means. In particular, neopterin, a general inflammation marker in the cell-mediated immune response (Th1-type), reacts to several viral and bacterial infections – reflecting current health status. In humans and captive animals, urinary neopterin levels correspond with serum, providing non-invasive means of monitoring progression and severity of disease. However, whether urinary neopterin measurements are sensitive enough to detect changes in health of wild populations under constant pathogen pressure is unknown. To determine this, urine samples collected during a respiratory outbreak were compared with control samples collected before and after the outbreak in a group of wild chimpanzees (*Pan troglodytes*) in Taï National Park, Côte d'Ivoire. Respiratory diseases often result in high morbidity and mortality in great apes – disrupting normal social dynamics with short- and long-term implications. During this outbreak, 32 of 37 individuals exhibited respiratory symptoms (e.g., lethargy, coughing, nasal discharge). Fourteen individuals died as a result of the disease. In comparison to pre-outbreak levels, urinary neopterin levels significantly increased during the outbreak corresponding with observed symptoms. We conclude that urinary neopterin is a promising biomarker for investigating and monitoring health of wild primates with potential applications in the study of sociality, health and fitness.

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#### Behavioural Determinants and Consequences of a Sexually Transmitted Disease in Wild Olive Baboons (*Papio anubis*)

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Sexually transmitted diseases (STDs) represent a major ecological force in shaping the evolution of mammalian immune defence. STDs may further impact the evolution of mating systems. We investigated whether olive baboons (*Papio anubis*) at Lake Manyara National Park, Tanzania vary their sexual and social behaviour in response to mating partners which are infect-

ed by *Treponema pallidum*. This bacterium causes syphilis and yaws in humans and is often associated with anogenital ulceration in baboons of both sexes. It was first reported from LMNP in 1994. We quantitatively investigated mating behaviour to assess the effect of visible signs of infection (ulcerations) on mate choice. It was hypothesized that male baboons favour healthy looking females over severely infected partners. Our study group comprised 170 individuals (at least 35 adult males and 53 adult females) which were habituated to the presence of a human observer. Infection rate (as estimated by visible signs) was 51% and 53% in males and females, respectively. Preliminary results indicate that grooming and copulations were less frequent with severely genital ulcerated females. Olive baboon males usually compete for oestrous females which lead to consort take-overs. However, such take-overs occurred rarely in our group. Instead it was more frequent that consortships with a particular male and female lasted throughout the female's oestrus period and there was a high probability that the same pair established consortships in successive periods. Our data suggest that obvious handicaps due to the genital ulceration have an impact on sexual behaviour and mate choice.

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### So Happy Together? Ecological and Social Correlates of Stress in Wild Red-Fronted Lemurs (*Eulemur rufifrons*)

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Group living provides benefits such as reduction of predation risk and joint resource defense but also bears costs such as increased risk of pathogen transmission. In particular, social organization and social relationships can have a profound impact on the physiological stress response, which in turn plays a pivotal role in mediating the link between sociality and health. On the one hand, sociality can be a source of stress for individuals, as they have to deal with dominance and unpredictable changes in their social network. On the other hand, social support and strong social bonds can reduce the adverse effects of stress and improve an individual's health and fitness. We investigated ecological and social correlates of physiological stress in red-fronted lemurs (*Eulemur rufifrons*) in Kirindy Forest, Western Madagascar. Their social system deviates from that of the better-studied anthropoid species, with high levels of affiliation and social tolerance but also quite regular group takeovers and evictions upsetting social stability. We observed 32 adult individuals in 5 groups over a period of 18 months and collected regular faecal samples for glucocorticoid metabolite (fGCM) analyses. We focused on quality and quantity of social relationships and sex differences on fGCM concentrations. Preliminary results indicate that the dry season is characterized by elevated fGCM levels in all individuals. Reproductive season also impacted on fGCM, with increased fGCM concentrations found in females during gestation and early lactation, and during the mating season and the early lactation period in males. Finally, aggression rate was positively correlated to fGCM, while time spent in contact with a social partner showed a negative correlation with fGCM levels in both sexes, supporting the social buffering hypothesis in this species.

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## How Many Friends a Day Keep the Doctor Away? Health Consequences of Sociality in Verreaux's Sifakas

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Life in social groups exposes individuals to various health-related costs and benefits. Two major unavoidable costs of sociality have been identified: increased parasite transmission and more intense competition resulting in elevated stress levels. Both factors are known to cause health problems through increased susceptibility to infectious and non-infectious diseases and are modulated by social behaviours and group features like group size and social structure. However, many other variables can impact the consequences of sociality as well, limiting our current understanding of the trade-offs related to group living. Against this background, we conduct a comprehensive study examining relationships among group size, social interactions and various ecological and physiological variables in a wild population of Verreaux's sifakas (*Propithecus verreauxi*). We will present preliminary data on social behaviours ( $n > 600$  h focal observations), ranging patterns ( $n > 200$  days of GPS data), measures of faecal glucocorticoids ( $n > 600$  samples) and measures of parasite richness ( $n > 200$  samples) in 29 individuals of 6 differently sized groups (range 2–8). We will examine possible correlations among these variables with special focus on the effects of group size and social behaviours on individual health. Preliminary analyses revealed that group size did not influence individual physiological stress levels or daily travel distances. Interestingly, home range size was negatively correlated with group size, potentially indicating that bigger groups may occupy habitats of better quality. We expect to make a significant contribution to the general understanding of the costs and benefits of sociality. This study is part of the Research Group "Sociality and Health in Primates" and is funded by the "Deutsche Forschungsgemeinschaft (DFG)."

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## Social Determinants of Physiological Stress and Health in Wild Crested Macaques, *Macaca nigra*

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The quality and quantity of social relationships influence the individual risk of mortality in humans and animals alike. The buffering effect social relationships may have on acute and chronic stressors have been particularly invoked in this respect. Chronically elevated glucocorticoid levels have been shown to suppress the immune system and, thus, to increase susceptibility to parasites and disease, and thereby mortality in a variety of taxa. In our study, we investigated the buffering effect social relationships may have on acute and chronic stress in 2 wild groups of crested macaques (26 and 29 adult individuals), a highly tolerant primate species, endemic to Sulawesi Island, Indonesia, over a 12-month period. Thanks to the observation of grooming interactions and body contacts, we used social network analysis to evaluate individuals' social centrality within their group (weighted degree and betweenness centrality). We also considered scratching, yawning and self-grooming rates as behavioural measures of individuals' stress levels. Finally, we measured physiological stress by assessing faecal glucocorticoids

metabolites levels from faecal extracts. In accordance with studies on other mammal species, we hypothesize that occupying a central position within the social interaction network would be associated with lower physiological and behavioural stress levels. Indeed, considering the tolerant social style that characterizes crested macaques, being central within the social network of the group implies a high frequency of socio-positive interactions with different partners, which might increase the calming effect of body contacts and grooming. Moreover, this position might also provide more support during conflicts, helping to reduce aggression-related anxiety. We therefore hypothesized that these central individuals would cope better with social and environmental acute stressors, leading to lower chronic stress levels and ultimately a better health status.

## Symposium

### Updates in Primates Conservation

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#### Cultural Consensus as a Novel Method to Evaluate Behavioural Change in Conservation Education Programmes

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Conservationists recognise the urgency to increase the environmental capacity of local people living beside threatened habitats through long-term, evaluated education initiatives. Here we promote the use of Cultural Consensus Analysis (CCA) with associated free lists and domain analysis to evaluate a conservation education programme surrounding a children's picture book that we developed to increase knowledge about and empathy for an obscure Critically Endangered primate, the Javan slow loris (*Nycticebus javanicus*). We extracted free lists of key words from two essays each of 580 children during initial and final training sessions, conducted ~18 weeks apart. We gave each child a storybook highlighting ecological concepts about the target species at the end of the initial session, and asked him/her to write a second essay at the beginning of the final session to measure knowledge using Bloom's Taxonomy of Learning Domains. Children increased use of words accurately associated with the conservation programme exemplified by rises in salience; they also freely recalled terms used in the book, which comprised 76% of all terms in the final session. Using minimal residuals factor analysis, we found that domain coherence increased from 22 to 47% across schools. We identified 15 factors in 10 categories of terms contributing to the domain "Slow Loris"; "Loris Biology" was the category which showed the greatest increase (25 to 43%). Children achieved all 6 levels of Bloom's Taxonomy; in addition to knowledge retention, children generated unique stories and conservation opinions. Free from the constraints of questionnaires and surveys, CCA provides a promising avenue to evaluate behaviour change in conservation education programmes.

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## Primate Conservation in the Annamite Mountains with Project Anoulak: Recent Updates and Future Potential

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For the past four years, Project Anoulak has been developing and implementing projects in Nakai-Nam Theun National Protected Area (NNT) in central-eastern Laos. NNT is recognized at the national, regional and global scale for its importance for biodiversity conservation. It falls in the heart of the Annamite Mountain Range: one of the richest regions of Southeast Asia in terms of biodiversity and endemism and is one of the identified “key biodiversity areas” within the Indo-Burma biodiversity hotspot. NNT is notably home to 9 species of primates, including the largest population in the world of red-shanked douc (*Pygathrix nemaeus*) and white-cheeked gibbons (*Nomascus siki* and *N. leucogenys*). Project Anoulak has been involved in (1) capacity building of young Lao nationals and local communities; (2) community awareness raising with activities in village schools, teacher training and production of educational materials; (3) law enforcement with ranger patrols in the forest and with the training and employment of villagers from the local community and (4) scientific research. In the past four years, our data have demonstrated NNT to be one of the most important areas and best hope for the long-term conservation of the red-shanked douc and the white-cheeked gibbon. We have initiated the first long-term behavioural ecology study on both species and are currently collecting data on the distribution and taxonomic status of the southern and northern white-cheeked gibbon. We present an overview of our activities and results over the past four years and discuss the future potential of our project.

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## Conserving Non-Protected Primate Habitat: The Rungan River Conservation Programme of the Borneo Nature Foundation, Indonesia

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Unprotected forests are increasingly recognised as in need of conservation efforts. The Rungan River landscape is an extensive area of forest between the Rungan and Kahayan Rivers in Central Kalimantan and was, until recently, a conservation afterthought, with limited scientific surveys or conservation activities undertaken. Yet this forest block, at over 1,558 km<sup>2</sup> in size and close to the regional capital, is one of the largest relatively-intact forests in Bornean lowlands that (1) has no formal conservation area, (2) probably contains the largest orangutan (*Pongo pygmaeus wurmbii*) and gibbon (*Hylobates albibarbis*) populations that are found in an area designated for conversion to plantation: up to 2,000 orangutans and 9,000 gibbons and (3) includes significant endangered species populations such as the Sunda pangolin (*Manis javanica*), Bornean Bay cat (*Catopuma badia*), flat-headed cat (*Prionailurus planiceps*) and Storm's stork (*Ciconia stormi*). Borneo Nature Foundation conducted a landscape-wide survey of the Rungan River Forest in 2010 and 2016, to enable the status of the endangered and protected wildlife species of Rungan to be properly assessed and to determine areas of High Conservation Value and High Carbon Stock. Additionally, we are working to ensure community-engagement with these objectives and enable in-situ community-led conservation and to recommend measures for the sustainable development of this landscape that protects key biodiversity and prevents destruction of



Kalimantan's natural heritage. We will present preliminary results of these surveys, the importance of the forest at landscape level and highlight the community engagement activities underway. We will demonstrate how grass-roots conservation actions can lead to direct change in landscape conservation and how a multi-stakeholder approach can work to fully realise and maximise the conservation potential of the Rungan River landscape.

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### **Understanding the Social, Cultural and Political Context of the Primate Pet Trade: A Case Study of the Barbary Macaque (*Macaca sylvanus*) in Morocco**

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When developing a conservation strategy for a primate species threatened by the pet and tourist trade, it is important to understand the drivers of such trade. We examine the role of Barbary macaques as pets and photo props in Morocco. We conducted 20 confidential semi-structured interviews with 10 rural and 5 urban participants and 5 officials from the Moroccan wildlife protection department to understand their views of the Endangered Barbary macaque. We identified three emergent themes relating to participants' diverse perceptions of macaques. The position of primates in Islam was important to rural participants, none of whom kept a macaque as a pet. The urban participants, who kept macaques as pets, viewed their possession of the animals as a symbol of their financial status. Forestry officials viewed the macaques negatively due to their perception that the animals damage economically important trees. We interpret these findings in the context of a rapidly changing sociocultural situation and an increase in the national tourism industry in Morocco to explain the demand for the Barbary macaque as a pet, resulting in the drastic decline of the species in some areas of its distribution. We discuss why confiscating photo prop macaques and fining their owners is not having the desired effect of dissuading photo touts from purchasing other macaques to continue their trade in the Tangier-Tétouan region. We suggest that legal mechanisms may be ineffective in Morocco because public awareness of wildlife conservation and welfare is very low. We are countering this trend by training and equipping Moroccan volunteers in 6 cities to raise public awareness about Barbary macaques and the negative effects of pet keeping and tourism on the species.

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### **Do Edge Effects Negatively Impact Arboreal Primates in Madagascar?**

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The progressive fragmentation of forest habitats causes a number of negative consequences that impact primate communities. It is widely understood that a decrease in fragment size entails an increase in habitat edge areas which in turn can result in potential structural changes of the forest habitat close to the edge. However, very little scientific research investigating the effects of these changes on primates has been conducted. The Sahamalaza sportive lemur, *Lepilemur sahamalazensis*, is a small, nocturnal and arboreal primate endemic to Madagascar. These critically endangered lemurs are dependent on intact forests for their survival. This study therefore focused on whether parts of their remaining habitat, and as a result the lemurs themselves, are negatively affected by changes in edge areas. By collecting data on temperature, humidity and light inten-

sity along transects we established an edge-core gradient for these abiotic variables and calculated a microclimatic “buffer zone.” This zone was influenced by the surrounding non-forest matrix and penetrated the fragment up to 165 m, leaving only 30% of the fragment unaffected by edge influence. There was no significant effect of these microclimatic changes on vegetation; the fragment was structurally variable throughout. From 770 h of behavioural observations of 14 individual sportive lemurs between 2015 and 2016, we established home range sizes, activity budgets and habitat use of animals inhabiting the edge area and those in the core forest. Animals living in the edge area used more trees with a DBH of less than 5cm ( $\chi^2_{(1,1129)} = 6.3, p = 0.01$ ) but there were no statistically significant differences in any other variables between edge and core animals. The sportive lemurs studied were not negatively influenced by the microclimatic transition zone, but more research is needed to establish the minimum requirements for habitat size and population sustainability in this species.

## Symposium

### Communicative Complexity in Non-Human Primates’ Gestural Signalling?

#### Complexity in Monkey Communication: Gestural Signalling in Red-Capped Mangabeys (*Cercocebus torquatus*) Is Intentional

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Communicative complexity in the animal kingdom can be assessed in a variety of ways. One way is to count the number of structurally and functionally distinct elements present in a species’ communicative repertoire. Another way to approach this issue is to investigate whether complex cognitive capacities, such as intentionality, underlie the communicative attempts of animals. It is now widely accepted that ape gestural signalling is intentional and highly flexible. However, such evidence is scant for monkey communication, especially when considering signals produced amongst conspecifics. Consequently, monkey communication is still often characterized as cognitively less interesting or less complex compared to ape communication. We present data on the naturally occurring gestural communication of 17 captive red-capped mangabeys (*Cercocebus torquatus*) living in 3 different social groups at the Station Biologique, Paimpont, France. When applying methods originally established in ape gesture research to assess whether these monkeys used “markers of intentionality” during their gesture production, we found that 24 out of a total of 32 different signal types (including 4 facial expressions) qualified as intentional. They were characterized by sensitivity to the attentional state of recipients and goal persistence. Our results reveal that monkey communication is cognitively more complex than previously assumed, and show that the precursors to flexible and intentional communication were already present in the primate lineage around 30 My ago.

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## The Multiple Timescales of Ape Gesture: Reconciling Evolution, Ontogeny and Iconicity

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A crucial aim of ape gesture research is to understand how apes acquire and use the particular gestures in their inventory. Many studies have focused on whether gestures are biologically inherited or develop from the ontogenetic ritualization of instrumental actions, e.g. reaching, while a few studies have proposed that some gestures might be iconic. Here, I examine ape gesturing as the interaction of processes occurring at multiple timescales of evolution, ontogeny and real-time interaction. I argue that gestures stem from the phylogenetic and ontogenetic ritualization of actions, and from the simulation of actions that are desired during real-time social interaction (i.e. iconicity). To support this claim, I present analysis of gesturing by gorillas, especially captive western gorillas (*Gorilla gorilla gorilla*) at the San Francisco Zoo, and the enculturated western gorilla Koko (at the Gorilla Foundation, California). In particular, I look at two cases: (1) directive positioning and scratching gestures used by one gorilla to guide another's actions and movement, and (2) more elaborate pantomimes of actions produced by Koko and other enculturated apes. In both, I show how a single process such as phylogenetic or ontogenetic ritualization cannot explain the considerable variability in the form of any particular gesture as it is used in context. Conversely, iconicity cannot provide an adequate account of the highly stereotyped and stylized forms of many recurring gestures. I conclude that ape gestures exhibit a balance between forces of ritualization – both from innate biases endowed by evolution, as well as from repeated use in ontogeny – and of iconicity deriving from the simulation of desired actions, which infuses contextually relevant variability into gestures. In each case, the root of ape gesturing rests in the communicative transformation of instrumental actions across multiple timescales.

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## Developmental Effects on Gestural Employment of Chimpanzees in the Wild

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To understand the complexity involved in animal signalling, studies have mainly focused on repertoire size and information conveyed in signals of birds and non-human primates. However, recent studies on vocalizations and gestures of non-human primates have shown that we also need a detailed understanding of communicative development and its relation to the social environment to grasp this phenomenon in detail. Here, we examined gestural signalling of chimpanzees, *Pan troglodytes*, living in two communities in the wild (Kanyawara, Uganda; Tai South, Côte d'Ivoire) with a special focus on the influence of social exposure on signal development. Specifically, we investigated to what extent specific social factors, namely behavioural context, interaction rates and maternal proximity, affect gestural production (i.e. gesture frequency, sequences and repertoire size). We used a combination of video recordings and focal scans obtained from 11 infants aged between 9 and 69 months during 1,145 h of observation throughout two consecutive field periods. Overall, we found that social play was the context in which the highest

number of gestures occurred. Gesture frequency and repertoire size increased with higher interaction rates with non-maternal conspecifics and the number of previous interaction partners, respectively. However, no effect on gestural production was found for interaction rates with mothers. Our results thus imply that infants of social mothers may have a head start in life. Moreover, we provide hitherto undocumented evidence for sex differences in gestural signalling, which may reflect the differential importance of early socialization for chimpanzee males and females. Gestural development thus relies heavily on interactional experiences with conspecifics, which adds support for gestural acquisition via the learning mechanism of 'social negotiation' in great apes.

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## Studying Multi-Component Facial Behaviour in Primates

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One of the main features of animal communication is multimodality; conspecifics can receive and transmit information through a combination of visual, vocal, and olfactory behaviours. In primates, visual signals include gestures, positional behaviour and facial expressions. Facial expressions are typically combinations of multiple facial muscle movements caused by tension and/or relaxation in the face; each movement is referred to as an action unit (or AU). Each facial expression is associated with a unique AU combination, but AUs are used in many different expressions and are combined in different ways. Researchers use Facial Action Coding Systems (FACS) – a systematic method of identifying AUs – for examining the similarity between facial expressions. The development of FACS for humans, chimpanzees, orangutans, hylobatids and macaques has revealed species level differences in the presence and use of AUs despite sharing anatomical features. The multi-component nature of facial expressions and differential use across primate taxa raises new questions about communicative complexity. Should the absolute number of AUs and AU combinations within each facial expression be considered a measure of complexity? Or should certain AUs or AU combinations be rated as inherently more complex than others? Should contextual use be considered in determining the complexity of a signal? To help address these questions, we will present comparative analyses of facial expressions from two ape research projects. The first project examined the production of AUs and AU combinations under different behavioural contexts in hylobatids housed at the Gibbon Conservation Center. Results from this study suggest that the synchronous use of AUs and AU combinations is more important in the establishment of social bonds rather than the total number of AUs and AU combinations. The second ongoing project examines the use of AUs and AU combinations through a developmental approach by comparing repertoires of mother-offspring dyads in chimpanzees. The goal of this project is to explore how genetic relatedness, social bond strength, and/or behavioural contexts shape the use of certain AUs and AU combinations during an individual's lifetime. We will use data from both projects as an example of how future research can adopt both a multimodal and multi-component approach to understand primate facial behaviour better.

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## Combining Signals within and across Modalities in Great Ape Communication

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A crucial aspect of communicative complexity is the ability to combine different elements to create composite signals or sequences. These combinations can occur across modalities (e.g. a visual plus a tactile signal) or within modalities (e.g. 2 visual signals). Additionally, elements can be combined simultaneously or sequentially. We usually think of combinations of signals as bringing together 2 or more signals that are typically used on their own, but this may not always be the case. Elements found in composite signals may appear as independent signals, but it is also possible that some elements appear only in combinations, or may change form when used in combinations. In this talk, I will present video of gestural and multimodal communication of orangutans (*Pongo pygmaeus* and *P. abelii*) and chimpanzees (*Pan troglodytes*) from captive populations in the US and Europe. I will review methods commonly used to analyze multi-element signals, apply these methods to video examples of communicative acts and explore the resulting implications for interpreting signals as complex. In particular, I will compare signal combinations that occur within vs. between communicative modalities. Should we consider multimodal signals to be more 'complex' than unimodal signals? If so, what implications does this have for species-level differences in use of different communicative modalities? I will also ask whether all elements that appear in composite signals are also used on their own. Finally, I will compare multi-component signalling in great ape gestures to the combinatoric properties central to human language, with the goal of asking what the limits of element combination and reuse may be in great apes.

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## Complex Patterns of Signalling in Bonobo Communication: When Specificity Lies in Gestures

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In recent years, considerable progress has been made in our understanding of great ape gestural communication, with convergent evidence that gestures are produced flexibly and intentionally, that signallers take into account attention, comprehension and familiarity of their recipient, and that apes possess some of the key cognitive abilities required for language. However, the fact that gestures are often produced in combination with other signals has been largely overlooked. Multimodality is a core component of human language and cooperative communication, in which speech signals are routinely combined with other vocal and visual signals to convey or modify the speaker's intended meaning. We can therefore gain useful insights into the evolution of language by investigating the interplay between these two modalities in great apes' signalling behaviour. I will present three different studies on vocal and gestural signal combinations conducted on two different social groups of bonobos (*Pan paniscus*) housed at the Lola Ya Bonobo sanctuary (DRC). The results of these studies reveal that signal combination patterns vary and are sometimes specific to the signaller's intended goal. In general, we found that calls do not vary acoustically depending on the signaller's goal but serve to attract attention and inform about the social context and the emotional state of the signaller. Gestures, on the other hand, seem to be more flexible and used to further emphasize or specify the signaller's goal. These findings support

the idea that the common ancestor of modern humans and great apes probably communicated with a combination of gestures and species-specific non-linguistic sounds, with meaning being primarily conveyed by gestures.

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## **Do Chimpanzee Signal Combinations Provide Refinement or Redundancy in Meaning?**

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Chimpanzees, like many animal species, communicate using a wide range of signal types including: gestures, vocalisations, postures, and facial expressions; employing these singly and in combination with each other. To date, most great ape communication research has focused on individual signal types in isolation. However, we are now in a position to consider communication more holistically and look at signal combinations both within and between signal types. Here we investigate the gestural and vocal communication of the wild Sonso chimpanzee (*Pan troglodytes schweinfurthii*) community in the Budongo forest, Uganda. We recorded 6,739 signals produced within 93 h of focal follows on 30 individuals; and analysed these together with ad-libitum video data collection of an additional 2,000 signals. We describe how signal combinations are used by individuals of different age, sex and rank groups; and investigate whether or not signal combinations provide redundancy or refinement of the message transmitted. We discuss these findings in relation to the various socio-ecological challenges that chimpanzees are exposed to in their natural forest habitats.

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## **Gestural Turn-Taking: A Useful Means to Assess Communicative Complexity?**

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Humans use one of the most sophisticated communication systems in the animal world to engage in complex, coordinated and cooperative communicative interactions – language. Whereas comparative studies on communication systems of other animals have become a fascinating, highly interdisciplinary and empirically challenging asset for theories of language evolution, there are critical gaps in our understanding of communicative complexity – both at the proximate and ultimate level. The aim of the present paper is twofold. First, it will provide a brief overview of current approaches into communicative complexity (e.g. number of signals involved, estimation of the amount of uncertainty). Second, it will introduce a relatively unexplored research paradigm – cooperative turn-taking – and discuss whether it represents a useful asset to link properties of communication systems to complexity theory.

## Symposium

### 3D Imaging for Functional Studies in Primatology

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#### Is Ear Pneumatization Functional or Just a Heritable Trait?

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The morphology of the internal structures of the ear has been studied in primates for several decades. These studies describe parts of the outer, middle and inner ear, mainly for phylogenetic inferences. Over the past ten years, the development of high-resolution imaging techniques has made possible the access to internal structures, avoiding any risk of cranial damage. Data from 3D imaging allow qualitative and quantitative explorations of anatomical structures. Here we focus on the pneumatization of the middle ear cavities, which is highly variable in primates. The sample includes 115 specimens, belonging to 23 extant species (11 haplorrhines and 12 strepsirrhines). The degree of pneumatization is quantified by the ratio between surface and volume of the cavities. We tested the effect of phylogeny on pneumatization. Our results confirm the morphological differences between haplorrhines and strepsirrhines. The haplorrhines present greater variation in the degree of pneumatization than the strepsirrhines. The high degree of pneumatization is remarkable in Galagidea, comparable to that of some small haplorrhines. Additionally, we included in the analysis specific characteristics coding for biological, ecological and environmental information (life history traits, behaviours and habitat). First results indicate that the degree of pneumatization is significantly explained by body mass and activity rhythm. No significant results were found for weaning, longevity or locomotion. Covariations between the degree of pneumatization with some characteristics will be further investigated in order to identify the functional aspect of this trait and may highlight potential acoustic niches for some groups, and then be relevant for palaeobiological reconstructions.

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#### Shape and Function of the Hominid Auditory Region

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Computed tomography has revolutionized evolutionary studies of the human cranium, including the auditory region (external, middle, and inner ear) largely hidden inside the temporal bone. Previous studies have shown that modern humans are characterized by a distinctive morphology of the bony structures of the ear region (e.g. ossicles, bony cochlea) when compared with other primates, including great apes. However, quantitative data of the soft-tissue morphology of this region exist for only a few species and it is not clear to what extent the specific morphology of humans relates to their derived auditory capacities. Furthermore, drawing even basic morpho-functional conclusions is complicated by the notion that morphological differences may reflect allometry and co-variation between individual structures instead of function. A primary reason for unravelling the various factors is to obtain comparative information on soft tissue morphol-



ogy as well as the spatial relationship between the auditory structures. Here, we give an overview of our research focusing on the evolution of the auditory region of hominids (great apes and humans). Based on micro-CT and 3D geometric morphometrics (GM) we study 3D shapes and functionally relevant measures of the middle ear and cochlea. First, we review how geometry of the bony middle ear correlates with ossicle shape and function in extant and extinct hominids. Subsequently, we present a GM approach based on in situ soft-tissue visualization of the auditory region. Applied to 28 species, results of the GM analyses and examination of functionally important parameters (e.g. tympanic membrane area and basilar membrane length) show distinct differences in shape, size and spatial configuration of the ear region across primates, further emphasizing the derived morphology in humans. Our research thus provides a strong basis for reconstructing auditory morphology and function in fossil hominids. This research was funded by the Max Planck Society.

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### **Just a Matter of Size? The Influence of Cranial Size Variation on Ear Functions**

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The analysis of the influence of size on morphological structures at different taxonomic levels, so-called evolutionary allometries, is one of the basics in evolutionary biology. Body size is a major variable that correlates with several anatomical and physiological traits. We investigated the allometries for middle and inner ear anatomical structures in Primates. For these traits, previous studies have already established correlations with body size for mammals but never within orders. The order Primates presents a great variation in body mass and thus constitutes a model group to test allometries. The aim of this study is to estimate the effect of body mass and cranial size variation: (i) on middle ear size and volume and (ii) on morphological traits commonly used to infer auditory parameters, such as sound transmission, sensibility to high and low frequencies. We found a significant phylogenetic effect on size of the traits in the middle ear. Strepsirhines and haplorrhines show differences in ear dimensions with inflated bullae in the former and more reduced bullae in the latter. However, within suborder, size variations can be understood differently. Allometric patterns are very different between body mass classes, highlighting the thresholds of 500 and 6,000 g defined by Kay and Simons in 1980. Moreover, the bullae dimensions relative to the cranial length follow a negative allometry. No significant relationship is found when the bullae volume is standardised by the area of the tympanic ring. This result is probably due to a homogeneous regulation of air pressure between species. Results on auditory parameters indicate that the percentage of transmission is similar between species. Larger animals are more sensitive to low frequencies and smaller ones are more sensitive to high frequencies. Our results illustrate the importance of considering the allometric patterns in the evolutionary understanding of ear shape and function.

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## Geometric Morphometric Approaches to Infer Bite Force and Diet in Extinct Strepsirrhines

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The cranial system in mammals is highly constrained. Feeding forces, phylogeny and the need to protect the brain and sensory organs are all important factors driving the evolution of the shape of the skull. Here, we explore relationships between bite force, cranial and mandibular shape to infer the dietary ecology and bite force in two extinct species of strepsirrhines. We collected data on molar and incisor bite forces and analyzed cranial and mandible shape using 3D geometric morphometric approaches for 18 species of strepsirrhines that differ in feeding ecology. In addition, we use data on mandibular shape to infer the diet of two extinct species, *Archaeolemur edwardsi* and *Hadropithecus stenognathus*, and use the observed co-variation between bite force and mandible shape in extant taxa to infer bite forces in these taxa. Our results show that bite forces vary across species, with dietary specialists differing in bite force, cranial shape and mandibular shape. The covariation between bite force and mandibular shape was strong and based on these data we inferred molar bite forces close to those of herbivorous species in *A. edwardsi* and *H. stenognathus*. Finally, mandibular shape data demonstrate that both species were certainly folivores, supporting the most recent stable isotope data for these species. Supported by NSF-BCS-1062239 to C.E.W.

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## What Can the Shape of the Calcaneus Tell Us about Locomotion in Extinct Primates?

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The calcaneus of extinct primates has been used to infer locomotor behaviour in fossil forms, using features such as the elongation of its distal part. Distal calcaneal elongation has been associated with leaping specializations, as well as body mass. In this study we use 3D geometric morphometric techniques in order to assess the phylogenetic signal of the calcaneus as well as evaluate the covariation that exists between its shape and the type of locomotion, specifically the proclivity for leaping, and support use in extant strepsirrhines, taking into account the complete morphology of this foot bone. To do so, we use 3D surface reconstructions from Morphosource (<http://morpho-source.org/>) and locomotion and support use data from Oxnard and collaborators. Geometric morphometric data were taken on 30 calcanei of different extant strepsirrhines. We have focused on calcanei of extant strepsirrhines because they represent examples of early stages in primate evolution and exhibit locomotor repertoires specialized to very different environments. Studying the relationships between form and function of the calcaneus and applying them to the fossil record can clarify locomotor modes used by early forms. Our preliminary results show that the shape of the calcaneus has a moderately strong phylogenetic signal (calculated using a multivariate K), and that body mass also has an effect on the shape of this bone. Locomotion and the tendency to

leap have a strong phylogenetic signal. However, we find no significant phylogenetic signal for the type of support used during locomotion. The shape of the calcaneus and locomotion significantly covary within extant strepsirrhines, even when phylogeny is taken into account. The leaping strategy also covaries with the shape of the calcaneus, but only when phylogeny is not taken into account. Finally, support use and the shape of the calcaneus covary at a lesser degree than leaping and locomotor strategies. Thus, the shape of the calcaneus is not much affected by the type of support used in extant strepsirrhines, but it is affected by locomotor repertoire as well as leaping proclivity, even though the latter is more dependent on phylogeny.

## Symposium

### Social Networks in Primates: From Individuals' Attributes to Network Diffusion

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#### Fitness Benefits of Sociality: Macaques with More Social Partners Form Higher-Quality Sleeping Huddles

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Although there is mounting evidence that individual social integration is linked to offspring survival, longevity and reproductive success, the mechanisms that mediate these effects remain unclear. Here we investigate a potential mechanistic link between social integration and survival, using two groups of wild Barbary macaques (*Macaca sylvanus*) in Ifrane National Park, Morocco. More specifically, we investigated if an individual's position in the grooming network is linked to social thermoregulation benefits during adverse weather conditions. We found that adverse weather conditions, such as low temperature, high winds and precipitation, increased the size of social thermoregulation huddles. Furthermore, we found that individuals that were better integrated into their social network had access to sleeping huddles containing more adult individuals at night. Such higher quality sleeping huddles are likely to significantly reduce nocturnal energy expenditure. This study is the first to report a direct link between individual sociality and benefits through social thermoregulation, providing a potential energetic mechanism by which social bonds can enhance fitness.

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#### Age Differences on Affiliative Interaction Patterns and Social Roles in Wild Rhesus Macaque

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Social relationships at different life stages have a non-negligible influence on the current and future life of group-living animals. Primates, with prolonged life, are likely to have various tactics of social interaction to meet their needs in response to changes in environmental or physical con-

dition. What strategies individuals of different life stages use in social interaction, and whether an individual's position or role in its group social network change with aging are still under-investigated. Here we recorded 3 kinds of social behaviours (approach, allogrooming and social play) of a group of wild rhesus macaques (*Macaca mulatta*), including 14 juveniles, 13 subadults and 24 adults, by using the focal animal sampling method. We used social network analysis tools to examine age differences in social interaction patterns, social roles (initiator or recipient) and social position (central or peripheral) in the 3 affiliative social networks. Our results showed that rhesus macaques of different age classes have different social interaction tactics that may fit their current situation and demands. Younger animals prefer to allocate social time to many group mates, which may help them to acquire survival skills; while older animals prefer to focus on several fixed partners, which may be a good strategy to build steady cooperative relationships. As they grow older, individuals tend to be the recipient of approaches and the initiator in grooming interactions. Immature animals may play an important role in social cohesion and item transmission in a group, but they have often been overlooked in previous studies and should receive more attention in future research.

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### Using Social Networks to Study the Transmission of Novel Behaviour in Primates

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In recent years, several claims have been made for traditions or “culture” in non-human primates, referring to group-typical behaviour that is thought to have been passed on within each group by social learning. Others have questioned these claims, suggesting that genetic or ecological differences among groups might explain behavioural variation. These disagreements have led to the high profile “Animal Cultures Debate.” I will show how a recently developed statistical technique, network-based diffusion analysis (NBDA), can be used to help resolve the Animal Cultures Debate. NBDA infers social learning if the pattern of diffusion of a novel behaviour follows the social network. I will explain the logic underlying the approach. I will then show how NBDA elucidated an important role for social learning in the spread of a novel tool using behaviour, moss sponging, in a group of chimpanzees, *Pan troglodytes*, thus strengthening the case for culture in chimpanzees. Over the coming years, NBDA promises to play a role in determining the importance of social learning in a range of contexts and in a range of primate species.

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### Macaques, Networks and Parasites – (How) Do Network Positions Predict Parasite Transmission?

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The importance of individual social integration for various health measures are intensely studied and well understood; yet to date the underlying mechanisms, especially in wildlife, remain largely unclear. While correlations between social network positions (SNP) and the risk of

contracting transmittable diseases have been reported in various species, causality has rarely been established under natural conditions. In order to shed some light on the temporal and potential causal connections between SNP and infection risk, we capitalized on routine deworming treatment in 2 social groups of Barbary macaques (*Macaca sylvanus*;  $n = 77$ ) living under semi-free-ranging conditions at Affenberg Salem, Germany. Barbary macaques show highly differentiated social relationships which have been demonstrated to be beneficial for the individual. We aimed at disentangling the potential trade-off of these relationships with regard to susceptibility and exposure to gastrointestinal parasite infection. We collected  $\sim 3,700$  h of focal animal data to construct social networks and assessed parasite status by approx. weekly faecal egg counts ( $n > 1,400$ ) for all study individuals. While treatment successfully removed strongyle nematodes, the latency to first observed reappearance differed markedly between individuals, from  $\sim 3$  to  $< 12$  weeks. We will use network based diffusion analysis to investigate whether this variability can be explained by the individual's SNP, statistically accounting for factors influencing parasite susceptibility, e.g. age (age: 4–29 years), glucocorticoids levels ( $n = 1,290$ ) and physical condition measured via urinary c-peptides ( $n = 425$ ). Since high network centrality has been linked with higher parasite infection risk in primates, we expect more central individuals to acquire strongyle nematodes more quickly. We will test whether this pattern holds true for our study population and which network characteristics drive the transmission of or protection from parasite infection.

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## The Evolutionary Origins of Social Network Regulation

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All animals living in complex social networks that are characterised by expensive to maintain, intensive and long-lasting social relationships share the problem of managing the structure of these networks. For small groups this problem is trivial. However, for species with larger networks, most of which are primates, regulating the network structure is essential and complicated. This talk will focus on the different solutions to this problem, ranging from individual level management of ego-networks to social level regulation of the overall network structure of large groups. The results come from mathematical models of social networks, showing that social network building traits, evolved at the individual level, create a coordination problem for collective action taking place at the group level. The consequence is social network regulation. The talk will finish with empirical evidence for 2 different types of social network regulation in humans, and a prediction that such phenomenon exists in other primate species as well.

## 4 Posters Posters Cognition

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### An Object Choice Task Review

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Consistently poor performance by non-human primates (NHPs) on the Object Choice Task has led to claims that the comprehension of pointing gestures is a human-unique ability among primates, which may have contributed to the emergence of verbal communication. Recently it has been suggested that methodological flaws in the literature challenge the validity of such claims, and we develop and extend this to identify four key areas of inconsistency, pertaining to life history of subjects, barrier presence, inter-object distance and cue type. Individual data were available for 1,310 subjects of 36 species, comprising 9 taxonomic groups from 87 studies. Significant differences were found in the distribution of rearing histories across taxonomic groups, with 9% of NHPs being categorised as “close” on a human experience scale, compared with 93% of carnivores and 100% of human infants. Subjects from 4 taxonomic groups were tested with a barrier, including 100% of NHPs, compared with 5% of carnivores and 0% of human infants. Distance and temporal properties of cue types presented to subjects differed across the taxonomic groups, with 28% of cues to NHPs being *distal* compared with 76% for carnivores and 100% for human infants, and 75% being *dynamic* for NHPs, compared with 30% for carnivores and 64% for human infants. Inter-object distances differed significantly, with a tendency for NHPs to be tested with smaller distances than both carnivores and human infants. Significant effects on performance across taxonomic groups were found, with subjects categorised as “close” outperforming “occasional” and “seldom” subjects, and increased performance associated with *proximal* and *dynamic* cues, as well as greater inter-object distances. This review highlights the prevalence of incommensurate sampling and testing protocols across species and the need for greater consideration of ontogenetic influences on behaviour, rather than the current pervasive reliance on phylogenetic explanations.

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### The Missing Link: Developmental Experiences and Their Role in Studies of Social Cognition

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Hominoids (apes and humans) are strongly influenced by experiences during early development, resulting in behavioural variation in triadic engagements (e.g. joint attention, cooperation) in infancy. Contemporary scientists often under-estimate the contribution of developmental and emotional experiences to the formation of social cognition, which is especially problematic when

cross-species studies compare only 1 group of chimpanzees (e.g. those living in a sanctuary) and 1 group of humans (i.e. those living in evolutionarily unprecedented, post-industrial cultures). The variation in social cognition that results from different engagement experiences across groups, therefore, is misinterpreted as species differences. We offer a comparative design: multiple groups of chimpanzees with variations in rearing experiences compared with multiple groups of humans with variations in rearing experiences. This design embraces diversity in developmental engagement experiences across multiple human and ape groups. Consideration of developmental engagement experiences will contribute to more valid evolutionary theories of social cognition.

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## **Assessment of Directional Changes in Black Howler Monkeys (*Alouatta pigra*)**

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Primates' directional decision-making behaviour has been associated with the ability of finding food resources within complex heterogeneous landscapes. Because primates' ranging behaviour differs among species, the tools used to detect directional changes cannot be universally applied. Here, we aimed to determine which method is more appropriate to detect directional changes within black howler monkeys' movement patterns by comparing the Change Point Test (CPT) with a threshold of 45°. Both methodologies were used to test whether black howler monkeys perform (1) directional changes in-between routes as an indicator of a goal-oriented strategy to navigate, and (2) intra-route directional changes associated with feeding trees in order to monitor the phenological status of these trees while travelling to their next goal. Ranging data were collected during a 9 month study period in five groups of black howler monkeys at Palenque National Park, Mexico. The number of directional changes reported by the CPT (mean = 6.4/day) was significantly lower than for the method based on a 45° threshold (mean = 43.8/day). Most of the directional changes detected by the 45° threshold occurred within routes while the CPT detected a comparable number of directional changes within versus between routes. For both methodologies, black howler monkeys changed their direction after reaching a certain goal more often than expected by chance, suggesting a goal-directed-behaviour. The second prediction was verified using both methodologies as well, which showed that nearly 50% of the directional changes within routes occurred in trees where howlers had been observed feeding before. Although applying a threshold of 45° may overestimate the number of directional changes compared to the CPT, both methodologies led to the same conclusions and therefore can be applied equally to the study species.

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## **From Rote Memorization to Structure Extraction: Sequence Learning in Baboons**

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When reading the following three-syllable sequences, “ga ti ga” and “li na li”, we can memorize them as wholes but can also see that they share a common structure: in each the first and last syllables are identical while the second syllable differs. The processing of such “AB” patterns requires an extraction of the structural properties of the sequences, beyond the elements involved.



Crucially, this encoding allows generalization to isomorphic sequences made of novel elements. In humans, the ability to extract the structure of sequences is a key mechanism for high level cognitive functions such as language and reasoning. It is however unclear to what extent other primates possess this ability. Comparative studies have mostly tested the abilities of non-human animals to discriminate between sequences of the form AAB and ABA. These experiments suggest that numerous species share with humans the ability to detect immediate repetition of an element (e.g. the “AA” in AAB), but non-human species are unsuccessful with more complex regularities. In the current study, we developed a novel testing procedure to assess this ability in a group of guinea baboons (*Papio papio*,  $n = 19$ ). Unlike previous comparative experiments, we did not use an operant conditioning procedure, but an adaptation of an implicit learning task classically used with human participants. The baboons had to learn sequences of visual shapes, either of the form AA or ABA, in a serial response time task on a touch screen. A subset of baboons successfully learned both structures, and generalized their behaviour to isomorphic sequences made of novel shapes. These results suggest that the learning mechanisms underlying the ability to form abstract representations of sequences, a precursor of the ability to process syntax in language, were already present in our last common ancestor with baboons.

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### Which One Is Bigger? Perception of Visual Illusions in *Lemur catta*

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Perception of visual illusions has mainly been documented in birds and mammals, particularly in apes and monkeys. However, no research has focused on perception of visual illusions in prosimians. The aim of this study was to investigate whether 9 ring-tailed lemurs (*Lemur catta*) perceive the Delboeuf illusion, a size illusion. The study consisted of control and test trials, in which lemurs were required to choose spontaneously between two options. In control trials, we tested whether lemurs were able to discriminate between different amounts of food (the ratio between food portions was 0.66) on 2 identical plates. In test trials, the same-sized food portions were presented on plates of different sizes. If sensitive to the illusion, lemurs were expected to select the food presented on the smaller plate. Results showed that lemurs' choices did not differ significantly from chance in both control (% correct choices = 54%) and test trials (% correct choices = 44%). Therefore, ring-tailed lemurs do not seem to perceive the Delboeuf illusion. However, given the poor performance shown by the lemurs in control trials, further studies are needed to assess whether and how other factors might affect size judgments in prosimians.

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### Manual Laterality in Prosimians: News from the Ring-Tailed Lemurs

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Limb preferences seem to be widespread among vertebrates, including amphibians, reptiles, birds and mammals, suggesting an early evolution of these asymmetries. To trace the phylogeny of motor lateralization in primates, studies on a greater number of species are needed. Although

several researchers have investigated hand preference in monkeys and apes, fewer studies on manual lateralization have involved prosimian species, especially in experimental tasks. In particular, literature on prosimian hand preference for bimanual tasks is still lacking, although these tasks have been found to be more reliable measures of handedness in primates. Indeed, bimanual tasks have been found to elicit a stronger manual lateralization than unimanual tasks. The aim of the present study was to assess the hand preferences for a unimanual and a bimanual task in 17 zoo ring-tailed lemurs (*Lemur catta*), housed in Parco Natura Viva, Italy. In the unimanual task, they were constrained to use one hand to retrieve a food reward (primate jelly) inside an apparatus. In the bimanual task, lemurs had to keep the apparatus door open with one hand while reaching for food inside it with the other hand. Our results revealed a group-level right-hand bias for food reaching in both the unimanual and the bimanual tasks. Moreover, the bimanual task elicited a greater hand preference than the unimanual task. Our findings underlined the presence of a right hand preference in ring-tailed lemurs, providing new insights into the manual lateralization of prosimians. In addition, this study adds to the growing body of evidence that bimanual tasks are more suited to investigate primate manual lateralization, as they seem to elicit a stronger hand preference than unimanual tasks. As ring-tailed lemurs are the most terrestrial among prosimians, our findings suggest that terrestriality (and then bipedality) could have played an important role in the evolution of manual lateralization in primates.

## Poster Evolution

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### Gastrointestinal Helminth Infections in a Baboon Hybrid Zone

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Hybrid zones are natural laboratories for the study of speciation. The development of a stable hybrid zone will depend on the fitness of the hybrids. Studies of gastrointestinal parasites in primates are important, as parasites affect human and animal health, and parasite load may be linked to fitness. Our study took place in Awash National Park, Ethiopia, a well-studied baboon hybrid zone, where several groups of free-ranging olive baboons, hamadryas baboons and their hybrids roam. The goal of our study was to determine if there was a variation in the patterns of gastrointestinal parasite infection between the three populations of baboons (*Papio anubis*, *P. hamadryas* and *P. anubis* × *P. hamadryas* hybrids) living in Awash National Park. One hundred and forty six freshly defecated anonymous samples collected in 7 baboon groups from the 3 baboon populations were screened for helminth eggs by using a flotation method. In each faecal sample, we assessed the prevalence of eggs as well as the mean intensity of infection for *Trichuris* sp., *Enterobius* sp., *Strongyloides* sp., *Trichostrongylus* sp. and hookworms. The result of our study shows that helminth egg prevalence varies between the different baboon populations: olive baboons always had a higher prevalence of helminth eggs, hybrid baboons showed an intermediate prevalence of helminth eggs and hamadryas baboons always had a lower prevalence of helminth eggs. Quantifying the helminth parasite load could assist us in relating the level of infection to fitness measurements and co-adaptation of their genome and/or environmental influence. The environment as well as the genetics of the different populations of the Awash baboons differ and our study cannot disentangle which factors, environmental or genetic, are the most important drivers for gastrointestinal helminth infections. Only a longterm study will tell us the relative importance of each factor in explaining patterns of gastrointestinal helminth infections in the Awash baboons.

## Poster

### Human and Social Sciences

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#### **Aye-Aye, *Daubentonia madagascariensis*, Taboo of Killing in South Madagascar: A New Local Paradigm and No Evidence of Cultural Erosion with Infrastructural Development**

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Evidence of the aye-aye, *Daubentonia madagascariensis*, has been detected in the Tsitongambarika region, south Madagascar, providing an opportunity to evaluate the taboo of killing that surrounds the species in an understudied region. Previous studies of the aye-aye taboo have been limited to the northern and western regions. They often found that the aye-aye was reported to be a conveyor of curses or sickness or a symbol of death. Although tales vary between regions, there is a consensus that the aye-aye is regarded as an evil omen in Madagascar. The introduction of external belief systems, through the development of basic infrastructure, may play a role in the aye-aye being regarded as an evil omen. In order to assess this, we conducted interviews across 11 villages in the Iaboakoho District, in the northernmost section of the Tsitongambarika Protected Area, interviewing a total of 72 respondents who shed light on the local perception of the aye-aye. Villages were divided into 3 categories, based on the time taken on foot to reach them from the main road: <30 min, 30 min – 1 h, >1 h. This was done to establish a potential cultural erosion gradient. We did not find evidence of cultural erosion in the region. The responses highlighted that the killing of aye-ayes was taboo in the region as they were perceived as ancestors. The interviewees detailed the treatment of dead aye-ayes, including wrapping the corpse in white cloth, moving in a northerly direction across the island and placing monetary donations on the body. The respectful treatment of the species is echoed between villages despite the reason for such behaviours differing between households. This study sheds light on the reverential perception of the aye-aye in the south of Madagascar, presenting opinions and stories divergent from those that have been previously documented in the northern and western regions.

## Posters

### Conservation

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#### **The IUCN SSC Primate Specialist Group Section on Small Apes: International Collaboration to Conserve Gibbons and Siamang**

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The Gibbon Specialist Group, otherwise known as the IUCN SSC Primate Specialist Group's Section on Small Apes (SSA), is a group of gibbon experts from around the world that individually and collectively work to conserve gibbons. The SSA was set up in 2011 because of the serious

threat of extinction that gibbons face globally. Of 20 recognized species of gibbon, all are threatened with extinction on the IUCN Red List of Threatened Species, with 4 listed as Critically Endangered, 14 as Endangered and 1 as Vulnerable. The major threats to gibbons include loss of habitat and hunting pressure, often for the wildlife trade. The SSA is a group of more than 80 gibbon experts globally, with a shared vision of conserving the world's gibbons. The SSA contributes to gibbon conservation through: (1) strengthening coordination among gibbon conservation projects worldwide; (2) increasing awareness of scientifically-sound practice in gibbon conservation; (3) providing IUCN-endorsed guidelines to conservationists, field scientists and decision makers; (4) developing Conservation Action Plans that clarify priorities in gibbon conservation for practitioners, decision makers and donors; (5) ensuring the IUCN Red List of Threatened Species as a decision tool is thorough and up-to-date and (6) providing direct technical support to implementing projects engaged with gibbon conservation. Through collaborations with in situ projects, rescue centres and sanctuaries and ex situ zoos, the SSA works on the basis of sharing information and expertise. Key actions and outputs include workshops and technical skills meetings, Best Practice Guidelines, working groups on trade and disease and outreach through social media.

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### **Density of a Reintroduced Population of Bornean Orangutans (*Pongo pygmaeus*) in Pristine and Disturbed Forest Areas, Sungai Wain Protection Forest, East Kalimantan, Indonesia**

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The reintroduction of previously captive orangutans to the wild plays an important role in establishing orangutan populations in areas where they have been extirpated. In Sungai Wain Protection Forest, which is among the final extant primary lowland coastal forests in East Kalimantan, 82 formerly captive Bornean orangutans (*Pongo pygmaeus*) were released from 1992–1997. Forest fires burned approximately 60% of the reserve in 1998. The fires likely had a severe negative impact on this reintroduced orangutan population, as a nest survey conducted in 1998 after the fires produced an estimate of only 13–17 individuals remaining. Here we present data from a recent orangutan nest survey conducted in Sungai Wain Protection Forest. Line transects were used to conduct a nest survey in the area of primary forest, the regenerating area of forest, and an area of riverine forest. When an orangutan nest was located, the GPS location of the nest was recorded, as well as the distance from the bottom of the nest to the transect, the height of the host tree, the diameter at breast height of the host tree, the height of the nest above the ground, and the condition and features of the nest. The standard equations, which have been used in previous studies to estimate the population density of Bornean orangutans in Gunung Palung National Park, as well as Sumatran orangutans in Gunung Leuser National Park, were used to produce estimates for orangutan nest density and population density. The orangutan population in Sungai Wain Protection Forest appears to have increased significantly since the 1998 nest survey. Orangutan population density was estimated to be significantly higher in areas of primary forest than in areas of disturbed forest and riverine forest. This study produced an estimate of 35–40 orangutans currently inhabiting Sungai Wain Protection Forest. This study demonstrates the long-term success of an orangutan reintroduction programme, and we hope that it will provide valuable information for the many other orangutan rehabilitation projects across Indonesia and Malaysia.

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## Primates Traded as Traditional Medicine in Myanmar – A Tale of Three Markets

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Wild animals, including primates, are widely used in traditional Asian medicine, but quantitative data on prevalence, species composition and origin are lacking, especially for Myanmar, a country that because of economic sanctions, trade bans and ongoing internal conflict has been largely closed for research. Despite these constraints, we surveyed 3 open wildlife markets intermittently over 2 decades to assess the primate trade. We surveyed Kyaiktiyo, situated near the south coast, 4 times (2000, 2006, 2015, 2017); Tachilek, on the border with Thailand, 5 times (1999, 2000, 2006, 2009, 2013); and Mong La, on the border with China, 4 times (2006, 2009, 2014, 2015). We observed a minimum of 350 individuals of at least 5 primate species for sale. In Kyaiktiyo, mainly macaque, langur and hoolock gibbon skulls were on offer; numbers remained stable over time. Trade in Tachilek comprised mainly macaque and lar gibbon skulls; numbers declined over time. Trade in Mong La comprised freshly killed Bengal slow lorises, live northern pig-tailed and rhesus macaques, and parts of macaques, Phayre's langurs and lar gibbons. Trade in Mong La intensified over time. While all markets offer species from various regions of Myanmar or from abroad, information from vendors suggests most primates are caught locally. Bengal slow lorises, northern pig-tailed macaques and langurs and gibbons are globally threatened, and are legally protected within Myanmar. Ambiguities in Myanmar's primary legislation mean that while protected animals or their body parts cannot be traded, traditional medicine made out of them, can, provided it complies to rules related to the manufacturing of traditional medicine. Tachilek and Mong La are border markets and cater for Thai and Chinese customers, respectively. This international trade violates CITES regulations, and solutions to curb the illegal trade in primates and their parts has to be sought in collaboration with partners in China and Thailand.

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## Barbary Macaque Trade and Welfare in Moroccan Markets

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The Barbary macaque (*Macaca sylvanus*) is the only primate found north of the Sahara in Africa. Though once present throughout northern Africa and parts of Europe, its population is now highly fragmented and its current distribution is limited to small relict patches of forest and scrub in Algeria and Morocco. Barbary macaques are considered Endangered according to the IUCN Red List, with trade recognised as one of the major threats to the species. Morocco has recently adopted comprehensive laws relating to the keeping and selling of wildlife, though these laws do not appear to have diminished the trade. Morocco is also a member of the World Organisation for Animal Health and has proposed draft legislation prohibiting the mistreatment or abuse of animals in captivity. We surveyed wildlife markets and tourist squares in 20 cities and towns throughout Morocco in April to June 2013, April to May 2014, December 2014 and April 2016. We visited 13 markets once, but surveyed others up to 8 times over all 4 survey periods, focusing on larger cities, cities close to borders, and cities in which we had heard or read reports of wildlife trade. We found a consistent, open presence of macaques in Jemaa el Fna, the main tourist square in Marrakesh, on all 4 visits and received reports of pet and photo prop trade in Oujda and Meknes. Up to 11 monkeys, mostly juveniles, were kept at any one time in Jemaa el Fna, primarily for use as photo props but also offered for sale. The conditions in which the ani-

imals were observed clearly did not adhere to proposed welfare legislation. We recommend that Moroccan authorities fully bring in law 122-12 relating to animal welfare and enforce law 29-05 relating to wildlife trade.

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## **Disappearing in a Snap: An Investigation of How Taking Photos with Lemurs May Influence Tourists' Perceptions**

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The pet trade has been recently evaluated as a threat to the conservation of Madagascar's wild lemurs. While previous studies dealt mainly with how local people are involved in this pet trade, our research focused on what consequences tourism may have on the welfare and conservation status of lemurs. Tourists tend to consider taking photos of wildlife as an ecofriendly souvenir but it has been observed that: (1) photography can be stressful for the animal and (2) photos comprising humans and wildlife can influence peoples' perceptions of wildlife conservation. We decided to evaluate to what extent photos can influence tourists' perception of lemur conservation and desire to have a pet lemur. To explore these questions, on the basis of an Internet investigation into sites from which the higher tourist-lemur photos were emanated, we selected four sites for the research (Lemur Park, Lemur Island, Lokobe Reserve and Nosy Komba Reserve), each one visited for 10 days between the months of May and June. We focused on the lemur species that were most commonly photographed (*Eulemur fulvus*, *Eulemur macaco*, *Lemur catta* and *Varecia variegata*). At the entrance of every reserve we selected tourist groups using a convenience sampling method and for each group we collected data regarding tourist numbers, nationalities and ages. Every selected tourist group was followed in the reserve and data regarding their interaction with lemurs were recorded using an all occurrence sampling method; we also evaluated tourists' perceptions of lemurs and their desire to have a pet lemur through semi-structured interviews. Data were collected from a minimum of 10 tourist groups per site. We observed that tourists taking photos with lemurs were more likely to desire them as pets, showing that tourism including lemurs might need stronger regulations. These results have been presented to Madagascar's Tourism Board and will be a tool to improve lemur conservation.

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## **The Fruit of Discord? *Saba senegalensis* Use by Chimpanzees (*Pan troglodytes verus*) and Local People in the Dindefelo Community Nature Reserve (RNCD), Southeastern Senegal**

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Most research on human-primate interactions to date has focused on primate crop foraging behaviour and the costs of this for local people, with little attention on the co-utilisation of wild resources by sympatric humans and primates. However, this information is crucial to comprehensively evaluate the long-term nature and sustainability of interactions. Here, we combine

biological and social science methods to evaluate the importance of *Saba senegalensis* fruit to local people and Critically Endangered western chimpanzees (*Pan troglodytes verus*) in the Dindelo Community Nature Reserve, southeastern Senegal. This area is heavily impacted by humans and is a last stronghold for Senegalese chimpanzees. We estimate the amount of *S. senegalensis* extracted and assess spatiotemporal differences in its collection by people and chimpanzees. During *S. senegalensis* season (from May to July), there was a high presence of seeds in chimpanzees' faeces, demonstrating the importance of this fruit to apes. Likewise, *S. senegalensis* was also ranked as one of the most important wild plants by local people. Interviews revealed that *S. senegalensis* was harvested commercially to supply external markets, with profits used to purchase food and clothes. Local people and chimpanzees showed differences in the amounts of *S. senegalensis* gathered in different parts of the habitat. We discuss the sustainability of this practice and implications for the conservation of western chimpanzees in Senegal.

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## Environmental Education: A Tool for Primate Conservation in Ecuador

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Over the past few years, an increase in landscape changes due to human activity has been recorded. Deforestation, agriculture, farming, bushmeat and illegal trafficking of wildlife species alter Neotropical primate's ecology. Moreover, programmes for environmental education, research and conservation are very scarce. This can be seen in the Data Deficient conservation status of the IUCN Red List for some primate species. This project aims to enhance environmental education and to share scientific information, in order to encourage ecological values and to promote a culture of environmental awareness for the care and conservation of primates in Ecuador. This project was divided into two phases. The first one consisted of the implementation of a structured interview made up of 19 multiple-choice questions put together to evaluate the level of knowledge on environmental education, particularly the conservation of primates. We collected data from local people and tourists ( $n = 500$ ) in the towns of Fatima and Santa Clara (Province of Pastaza, Ecuador). Of the people surveyed, 30% ( $n = 150$ ) were between the ages of 30 and 35 years old. 80% ( $n = 400$ ) of the people surveyed indicated that they had never received any kind of environmental education and 95% ( $n = 475$ ) did not know the meaning of conservation. However, regarding the loss of biodiversity, the respondents considered that the conservation of the environment (97%) and conservation techniques (85%) can provide protection for primate species. The second phase involved the elaboration of an illustrated environmental education guide for any kind of audience. This guide was shared within the Fatima and Santa Clara communities in order to share knowledge and information on environmental education and the conservation of primates. This project raised awareness within the communities of the ecological role of primates in order to encourage people to care about their conservation.



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## Assessing the Impact of Volunteer Tourism on a Primate Conservation Project in Java, Indonesia

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Volunteer tourism is a type of alternative tourism in which participants volunteer under the structure of a host organisation which, in the case of conservation projects, usually involves the restoration of certain environments, researching society's attitudes towards environments, or engaging in empowerment and education of people. Small conservation projects of less known or less-charismatic species traditionally attract less conservation funding than those revolving around flagship species, and thus may rely on revenues generated by volunteer ecotourism. Here we examine how we developed a volunteer ecotourism programme for the Little Fireface Project, which focuses on the Critically Endangered Javan slow loris (*Nycticebus javanicus*) in Java, Indonesia. We launched our volunteer tourism in 2012. With a capacity of no more than 5 volunteers at a time, volunteers stayed for an average of 5 months (ranging from 1 month to 18 months), with an average of 17 volunteers per year. Monthly volunteer fees contribute on average to 15% of the cost of running the project, including costs such as rent and utilities that grants normally do not cover. Thirty one percent of volunteers were male and 66% were female, with an average age of 25, originating from 15 countries. Twenty eight volunteers also used their time to obtain an academic degree (8 = BSc, 15 = MSc, 7 = PhD). Volunteers contributed to data collection for an average of 28 h per week (20,664 total hours of data collection). Volunteers also contributed approximately 2,214 h to our education and community projects. Volunteers represent a valuable part of the conservation programme. Developing and maintaining a volunteer tourist programme has the potential to provide long-term funding for basic and applied research that may be difficult to obtain through more traditional routes.

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## Implementing Best Practice Guidelines: Barriers, Opportunities and Suggestions for Orangutan Rehabilitation and Re-Introduction Centres in Indonesia

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As land conversion, deforestation, and forest fires in Indonesia continue to contribute to the decline of wild orangutan populations, orangutan rehabilitation and re-introduction (R and R) centres have the potential to contribute to conservation by (1) successfully re-introducing rehabilitated orangutans into the wild and (2) promoting environmental sustainability in rescue centre construction through implementing practices into daily centre running and management. For this study, we visited three long-running, well-regarded orangutan R and R centres in Indonesia. Through questionnaires and interviews, in English and Indonesian, we determined the practicality of implementing the current IUCN *Best Practice Guidelines for the Re-Introduction of Great Apes* to orangutan R and R practitioners, and current and/or future centre environmental sustainability practices. We were then able to address the potential need for an updated, orangutan-specific addendum added to the guidelines. Questionnaires were designed with mostly open-ended questions to prompt descriptive answers. Interviews were held in a semi-structured fashion with those who completed questionnaires prior to the principle investigator's arrival at the centres. With the overall generality of the current IUCN guidelines, and the need for updates

found through this study, we identify the orangutan-specific information that was absent in the original guidelines and make a recommendation for the update of a new guideline based on suggestions provided by practitioners. We also identify the need for a multi-disciplinary approach to help rescue centres design and construct buildings which meet high sustainability standards.

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## Conservation of the Slow Loris, *Nycticebus* spp., at the Genetic Level: Phylogenetics, Phylogeography and Population Genetics

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Slow lorises (Strepsirrhini: *Nycticebus*) have a unique evolutionary history and are widely distributed in South and South East Asia, yet their taxonomy, evolutionary history and biogeography remain poorly understood. In this study, we report the largest study of the molecular phylogeny of the species in Vietnam. We analysed 60 samples by sequencing three mitochondrial genes, cytochrome b (cyt-b), NADH dehydrogenase subunit 4 (ND4) and cytochrome c oxidase subunit 1 (CO1). Also, in order to investigate genetic relatedness within and between populations in the slow lorises' range, we developed species-specific microsatellite markers of *Nycticebus* for the first time, sampling three model species: *N. javanicus*, *N. bengalensis* and *N. pygmaeus*. This was done using Next Generation Sequencing technology. Our results reveal clear genetic divergence between populations of *N. pygmaeus* from northern and southern Vietnam. Furthermore, a hybrid zone of pygmy lorises in central Vietnam is assumed to exist since the samples collected in the area can be divided into northern and southern subclades with high statistical significance. However, this hypothesis is intriguing and needs further investigation. The mitochondrial phylogeny agrees with recent studies on divergences of Lorisiformes and supports *N. pygmaeus* as the first to separate in the group (c. 11 Mya). The discovery of microsatellite markers allows us to assess the impact of extreme fragmentation on Javan slow loris populations and to analyse genetic variability within Vietnamese populations. The results obtained enhance reintroductions and captive management and help identify poaching hotspots. We urge further capacity building to support the application of genetic studies to the conservation biology of these animals.

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## Adaptive Habitat Strategy for the Slow Loris (*Nycticebus javanicus*) Living in a Fragmented Agroforest

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Wildlife crossings such as green bridges, live fences, hedgerows and highways are conservation strategies devised in response to fragmentation. Wildlife crossings increase connectivity to areas that provide habitat for numerous taxa but until now few studies have evaluated the utility of wildlife bridges for primates. Here we evaluate the use of wildlife crossings as a habitat strategy for the Critically Endangered Javan slow loris, *Nycticebus javanicus*, studied continuously since 2012 as part of a long-term study of their adaptation to an agroforest in Cipaganti, West

Java. We sent a questionnaire (regarding bridge materials, mammals that use them and duration of time to use) to conservation projects to gain an understanding of wildlife crossings, receiving 12 replies. We then analysed a behavioural dataset of 46,049 observation points, and determined that slow lorises used existing wildlife crossings in the form of raised hose pipes 199 times. To improve connectivity, we employed an additional 7 rubber bridges. We examined the impact of sex, age and abiotic factors on bridge use. We found that although both sexes used bridges equally, adults used them the most, with juveniles using them more than subadults. Slow lorises also used bridges more frequently on nights with less wind, less fog and a darker moon. Bridges were the third most common single substrate that slow lorises used, they are highly reliant on canopy continuity and grasp an average of 2 branches (range 1–9). Avoidance of bridges at more dangerous times such as light moons and adverse weather conditions show that predation or falling may play a role in use of wildlife crossings. The frequent use of such crossings also indicates that the risk of using them may outweigh the danger of travelling on open ground. Long term analysis on how bridges effect gene flow and mortality rates would benefit wildlife crossing projects, and such a project will be implemented at the site in Java.

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## The Cytotoxic Effect of Slow Loris (*Nycticebus*) Venom on Human Cancer

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Within the Kingdom Mammalia, venom evolution is rare, occurring in only 6 orders. Arguably the most cryptic and academically neglected venom occurs within primates among slow lorises (*Nycticebus* spp.). Venoms comprise novel biological compounds with a potential plethora of proteins and peptides available for utilisation in bio-medical research. We collected samples of slow loris saliva from eight captive-bred pygmy slow lorises (*N. pygmaeus*) at Paignton Zoo and Shaldon Wildlife Trust UK, given voluntarily when slow lorises chewed on Salimetrics children's swabs. From January to March 2017, we employed MTT assays, and microscopy assessments to determine cell survival on human epidermal carcinoma cells (A431 line) after the application of concentrations of slow loris salivary venom. Cell survival from both male and female derived saliva was half that of untreated cells. Cytotoxic action is demonstrated in concentrations as low as 0.1% venom. Results demonstrate a cytotoxic effect with ensuing physiological damage on human cancer cells, demonstrating the cytotoxic action of slow loris saliva only, without the admixture of brachial gland exudate. We show that even captive-bred slow loris saliva harbours potentially dangerous substances, with functional applications in slow loris husbandry. Knowledge of slow loris salivary venom increases understanding of the novel salivary composition and supports discussions of slow loris conservation by proposing a functional narrative to oppose the illegal pet trade, by contradicting their "cute and cuddly" appeal. Evidence of salivary venom shows that cytotoxic effects can result even in the absence of a bite puncturing the skin, and further demonstrates their inappropriateness as pets.

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## Efficient Workshop Design as a Key Factor for Conservation of Many Species

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Since 2007 the Little Fireface Project (LFP), has created workshops that aim to enhance knowledge about the slow loris (*Nycticebus* spp.) in South East Asia to help curtail their trade. All slow loris species currently listed on the IUCN Red List are Vulnerable or Critically Endangered, due to habitat loss and illegal trade. International trade hubs include Japan, the Middle East and Russia but local trade is common and under-studied, with social media increasingly being used to sell animals instead of open wildlife markets. We organized a workshop in Brunei with officials from the government and local NGOs to create awareness about slow lorises and increase conservation efforts. We evaluated the knowledge of 28 participants during a one-day workshop on the 2nd of March 2017 and 18 participants during a field-training day on the 4th of March. The knowledge of the participants was evaluated the same day using pre- and post-questionnaires, as well as group activities during the workshop. Analyses using Wilcoxon Signed-Rank tests indicated that the workshop created statistically significant changes in knowledge concerning the slow loris. We confirmed the efficiency of resources used during the workshop, presentations using pictures and videos, a leaflet to identify the different species and flash cards; for example 7 versus 83% of respondents could identify species correctly before and after the workshop, respectively. The results also provide information about trade in Brunei, with 68% of the respondents reporting slow lorises in anthropogenic settings, someone's house (24%) and wildlife markets (31%) ranking the highest. This study and other workshops organized by LFP reveal the importance of providing training to key stakeholders in preventing trade, and show that significant knowledge can be obtained after 1 day. Workshops and training in the identification of species are vital to make sure all stakeholders working to protect animals have the same level of knowledge and are aware of new scientific findings. We hope the work done by LFP can serve as a model that can be adapted to other threatened species.

## Posters

### Social Behaviour

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## Variation in Intra- and Intersexual Relationships in Closely Related Species of a Nocturnal Primate Radiation (*Microcebus* spp.)

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In diurnal primates, with their complex societies, egalitarian to despotic social relationships are established and maintained via agonistic conflicts, allogrooming, and coalitions as well as by spatial affiliation. Whereas much is known about the diversity and evolution of social relationships in gregarious primates, much less attention has been paid to nocturnal species, living in dispersed social systems. The aim of our study was to gain insight into the variation in male-male and male-female relationships in a nocturnal primate radiation, using the Malagasy mouse le-

murs as a model. We explored the patterns of inter-(male-female) and intra-sexual (male-male) interactions among 3 closely related mouse lemur species (*M. ravelobensis*, *M. bongolavensis*, and *M. myoxinus*) at 3 sites in northwestern Madagascar using a standardized social encounter paradigm. For the experiments, animals were trapped and temporarily kept in cages for up to 1 week. Six intra- and 6 intersexual pairs were observed per species, each for 3 h at the beginning of their activity period, over 6 consecutive days (18 h in total). Direct observations were conducted with all occurrences sampling of feeding, marking, vocalizations, agonistic and non-agonistic social behaviour of both pair partners, as well as by scan sampling of spatial affiliation. Dominance was determined by comparing the number of won and lost conflicts between the dyad partners. First findings indicated that within each species, females won more conflicts than males in 3 out of 6 male-female dyads. In contrast, social relationships among males within species were more variable. No difference in inter- and intra-sexual conflict rates was detected in 2 species, but a prominent difference existed in 1 species (*M. bongolavensis*). Based on this study, weak female dominance is suggested for all 3 species, which underlines that female dominance represents a much more flexible trait among mouse lemurs than previously expected.

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### **Behavioural Change of an Immature Male Golden Snub-Nosed Monkey in a One-Male Unit following a Social Fluctuation in the All-Male Unit**

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Social cognition abilities are highly developed in primates. According to Kummer's scheme, non-human primates can make effective judgements about partner choice to develop valuable relationships with useful social partners. In this study, we focused on a troop of captive golden snub-nosed monkeys (*Rhinopithecus roxellana*) in Shanghai Wild Animal Park, China. Behavioural instantaneous sampling was conducted on a single immature male of the one-male unit (OMU,  $n = 7$ ) and individuals of an all-male unit (AMU,  $n = 7$  or  $8$ ), for a total of 74 days, 540 h from January to June 2015. After 45 days of observations (322.5 h), the alpha male of the AMU was replaced due to a change in group dynamics and the unit split into 3 sub-units. We found that the social interactions of the immature male in the AMU declined significantly (U Test,  $p < 0.001$ ) after this social fluctuation. Before the fluctuation, he spent much more time with the alpha male and the sub-adult male than with the older one (Friedman Test,  $p < 0.001$ ), and he had some preferred social partners among juveniles in the AMU (Friedman Test,  $p < 0.001$ ). After the fluctuation, he spent more time in the sub-unit with the new alpha male (Friedman Test,  $p < 0.001$ ) than in the other two sub-units. These results suggest that the male juvenile seemed able to adjust his behaviours following the social fluctuation in the AMU. He might not only recognize the dominance rank orders in other units, but could also make use of his knowledge of third-party relationships when he choose social partners, which might be crucial for his potential alliance in the future. This study is a brief report of juvenile preference that should be studied more fully in large wild groups given this preliminary evidence.



affiliative interactions depend on *anxiety* (from calm to tense), which in turn is modulated by *kinfactor* (the coefficient of relatedness between two given agents) and depends on *stepdom* (a scaling factor from 0 to 1 and analogous to intensity of aggression). In egalitarian societies (i.e. low *stepdom*), engaging in an affiliative interaction depends mainly on *anxiety* because the influence of kin bias is weaker. Instead, in despotic societies (i.e. high *stepdom*), engaging in an affiliative interaction depends both on *anxiety* and *kinfactor* when the coefficient of relatedness between two given agents is high. To assess the model, we compared our simulation results with empirical data collected at the Primate Centre of Strasbourg University in a semi-free-ranging group of *Macaca tonkeana*. The simulation results agreed with the social structure values showed by the group of *M. tonkeana* (for example, low values of unidirectionality of aggression and high values of grooming reciprocation and post-conflict affiliation behaviours). A-KinGDom ABM may accurately characterise social structure patterns shown by macaque societies and can be used as additional information to develop management strategies in captive or semi-free-ranging groups.

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### **Analysis of the Social System of a Captive Group of Guinea Baboons (*Papio papio*): Investigating the Driving Forces of Sociality in Primates**

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In order to understand the “deep structure” of social systems, that is, the driving forces behind the regularities, in term of social traits, observed across species, we need observations of a large number of different groups. Among primates, baboon species are of particular interest due to their close phylogenetic proximity and their high ecological and social diversity. Very few studies have been conducted on the social system of Guinea baboons (*Papio papio*), yet they seem to display high ecological and sociological flexibility, combining features of other baboon species’ typical social systems. In the present study, we describe the social system of a captive multi-male/multi-female group of 90 individuals, by assessing its social organization, social structure and mating patterns. Our study reveals preferential spatial associations within the group and supports the multi-level system observed in some other baboon species. First, individuals associated preferentially with the opposite sex, forming organizational spatial units composed of one male and one or more females and juveniles, i.e. One-Male Units (OMUs). Social interactions between males and females were virtually restricted to within OMUs. Second, mating patterns reflect typical OMU-based systems as almost all females mate exclusively with their OMU male. Third, males do not seem to constrain female spatial relationships via herding and aggressive behaviours as in hamadryas baboons. Hence, it seems that OMU cohesion is likely to depend on affiliative behaviours between partners. Finally, male-male relationships are predominantly tolerant and we do not observe a linear hierarchy. Results from our group support findings on other wild and captive groups of Guinea baboons and confirm the idea that this species combines characteristics of different baboon social systems, creating a unique system where male-male relationships as well as male-female relationships seem to rest on mutual interest and tolerance.



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## Variation in Strength of Juvenile-Mother Bonds and Oxytocin in Wild Juvenile Chimpanzees

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In mammals, oxytocin (OT) is important for the onset and maintenance of maternal care and the mother-offspring bond and it is also associated with social bonds among adults. Here we are interested in the transition phase of juvenile chimpanzees, in which they become increasingly independent of their mothers. Although juvenile-mother bonds are generally strong there is still considerable inter-individual variability. We are interested in whether any differences in the strength of the bonds juveniles form with their mothers are associated with corresponding differences in OT levels, predicting a positive relation between OT levels and bond strength. We conducted focal sampling on 14 wild juvenile (5 to 11 years old) chimpanzees (*Pan troglodytes schweinfurthii*) from the Sonso community of the Budongo Forest, Uganda. We continuously recorded social interactions with the mother and other individuals, 15 scan samples of the distance to the mother and several measures related to the number, identity and distance of individuals present in the party with the focal subject. We also collected urine samples to assess OT levels using an enzyme immunoassay. We calculated a juvenile-mother bond index to compare bond strength in different juveniles. We then tested how these indices were associated with urinary oxytocin levels following social interactions with the mother. Our data fill an important gap in our understanding of the formation and maintenance of social bonds and will contribute to our knowledge of the evolution of social bonds in mammals and humans.

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## Do Same-Sex Mounts Function as Dominance Assertion in Male Golden Snub-Nosed Monkeys (*Rhinopithecus roxellana*)?

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It has been hypothesized that same-sex mounts can reflect the dominance relationship in a mounting dyad. Previous studies have found that mounting and being mounted were demonstrations of dominant and subordinate status, respectively. In this research, we aimed to test whether same-sex mounts function as dominance assertion in male golden snub-nosed monkeys (*Rhinopithecus roxellana*). We investigated this behaviour in 8 individuals (2–3 adults, 1 sub-adult, 4 juveniles), from a captive all-male unit (AMU) in Shanghai Wild Animal Park, China. Behaviour-dependent and all-occurrence sampling were conducted with a total of 1,855 mounts (922 occurred between juveniles and 933 occurred in other mounting dyads.) recorded from November 2014 to June 2015, a period during which the alpha male was replaced at the beginning of April. We built General Linear Mixed Models with age class of mounting dyads, social context, solicitation and rank difference as predictor variables and mounting dyad ID as the random factor. The three social contexts were peace, play and aggression, which were determined by behaviours of the mounter and mountee, or their social background. In support of the dominance assertion hypothesis, we found that during the entire study period, the higher-ranking males were more

likely to be the mounters than the lower-ranking ones, except for the mounts that occurred among juveniles in peaceful and playful social contexts. Our study indicates that the dominance relationship between two individuals engaging in mounting interactions can be influenced by the age class of the participants and the social context in which mounting occurs. We suggest that same-sex mounts might have different functions in different age groups and be multifunctional in a species.

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## How Does Castration Change Integration of Immature Males in Their Familial Group Network in Captive Western Lowland Gorillas?

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The European captive population of western lowland gorillas has successful breeding results and a healthy population development. With a harem social lifestyle and a balanced sex ratio at birth, management of the overpopulation of males begins to be problematic. For almost 20 years, bachelor groups have been established in zoos in order to counterbalance this trend but this solution is nuanced over time because of the recurrent agonistic conflicts recorded. This is why the European Endangered Species Program (EEP) considers castration as an alternative to manage the longevity and welfare of the captive population. This proposal has been made assuming that the mature castrated males may remain in their native family group in the presence of the silverback male without risking conflicts over access to females. Ten immature males have been castrated in 6 different institutions following the recommendation of the EEP committee. We collected all affiliative behaviours performed in proximity to one congener for 75 individuals of all age and sex classes living in 7 captive breeding groups (375 h of focal animal sampling, 5 h per individual). Among them, the results of 10 castrated immature males are compared to 10 “intact” immature males (five juveniles and five subadults in both categories compared). The analysis and visualisation of the different social networks provide precious knowledge of the social integration of immature ‘intact’ males in captivity. Moreover by comparing activity budgets and personality using the Gorilla Behaviour Index (GBI), “social preference” (contact or 1 metre proximity, instantaneous sampling) and “tolerance” (1 to 5 metres proximity), this study showed that castration has an impact on the socialization process of immature male gorillas, which are more cohesive in their group during maturation. This study also helps us to understand whether castration could be an acceptable tool to regulate the male overpopulation in captivity.

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## Living Area, Preference of Vertical Strata and Daily Activity of a Group of *Cebus albifrons* in Misahuallí, Napo, Ecuador: Preliminary Results

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At Misahuallí, Ecuador, there is a group of *Cebus albifrons*, a Neotropical primate, which is exposed to pet attacks, electrocutions, and food poisoning due to its coexistence with the villagers. The lack of information about the groups socioecology makes it harder to establish a specific programme of conservation. The aim of this study was to collect information on home range, preference of vertical strata, feeding behaviour and daily activity of this group (9 individuals), in order to better understand its ecology and to develop suitable conservation strategies. The group was followed from 7:00 to 19:00 for 12 days during March 2017. Its location was registered every 20 min with a GPS. Home range data were calculated with the minimum convex polygon (MCP) and the Kernel extension of the ArcGIS software. Data on vertical strata were based on height records using the following intervals: 0, 0 <1, 1 <3, 3 <5, 5 <7, 7 <10, and ≥10 m. Behavioural data were collected using instantaneous focal sampling and scan sampling. During behavioural observations, ad libitum feeding records were collected whenever animals were observed feeding (chewing or when they placed an item into their mouth). A total of 144 h of observations was collected by two observers (an interobserver reliability test was done). We found a home range of 4.9 ha with the MCP and 1.6 ha with the Kernel model. The preferred vertical strata for this group was between 3–5 metres (55.7% of time spent at this height). The distribution of activities was: foraging and eating (38.6%) followed by social activity (30.4%), resting (16.8%) and moving (14.2%). The diet (581 records) was based on fruits (50%), vegetables (12.3%), insects (11.6%), eggs (5.6%), bread (5.6%) and other products given by people or taken from garbage (14.8%). We found that this group does not move away from the town. Humans influence the monkeys' diet by providing unconventional food. Our results could help the local authorities to establish initial conservation measures.

## Posters

### Manipulation & Locomotion

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## Grasping in Platyrrhines: Variability Explained by Arborealism, Phylogeny, or Claws versus Nails?

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The prehensile abilities of the catarrhines have been studied, in particular to understand the cognitive, functional and evolutionary mechanisms that control behaviours, such as feeding. Among platyrrhines, capuchins possess a pseudo-opposable thumb and are known to use a great

variety of prehensile strategies. However, prehensile abilities are under-studied in other platyrrhines, which show a wide variety of ecologies and morphologies. In this study, we aim to determine quantitatively the different prehensile strategies used by 11 species of platyrrhines during their collection of non-mobile food-items of different sizes. The link between prehension and parameters such as the degree of arborealism and the presence of claws or nails, has been tested. Different patterns of prehension were observed and our results showed that (1) platyrrhines do not have only one stereotyped pattern of prehension, but several patterns that are sometimes complex. As a result of its high variety of precision grips, the capuchin remains distinct. However, other species without an opposable thumb seem to show an individualization of fingers (i.e. the ability to move each finger independently) that allows for complex prehensile strategies. Moreover, a hand preference was observed in some species. We also found (2) that the strategies of prehension, in terms of organ used and grip type, depended on the size of the food item: for big items manual and power grips were favoured, for small items the mouth and precision grips were favoured. In addition, we found (3) the degree of arboreality and the presence of claws or nails seemed to influence the prehension patterns: strictly arboreal species used more manual and power grips, partially arboreal species favoured mouth and precision grips. Species with claws used a mouth grip more and species with nails used a manual grip more. Possessing claws seemed to impact the variability of the grip types used but not manipulative capacities. More closely related species do not always show the same pattern of prehension, suggesting that prehensile strategies are not determined by phylogeny.

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## Anatomical Adaptations to Conflicting Functional Demands in the Primate Thumb

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The enhanced dexterity of modern humans is largely owed to the high mobility of the thumb. Adapting towards mobility, however, is in direct conflict with the thumb's preceding function in locomotion, as mobility is a trade-off for stability. Despite the loss of its locomotor function, stability of the human thumb joint remains important as the human hand is also employed to execute forceful precision and power grips. By comparing the anatomy and biomechanics of the thumb in non-human primate species employing different locomotor types, we seek to contribute to the understanding of functional adaptations in primate thumb anatomy. Our study focuses on the bipedal human, the knuckle-walking bonobo (*Pan paniscus*), the brachiating gibbon (*Hylobates* sp.) and the digitigrade baboon (*Papio* sp.). A full quantification of the soft-tissue architecture (thenar musculature and ligaments) and the external and internal bone morphology is collected from each species to identify relevant interspecific variations. State-of-the-art imaging techniques (microCT, CT and MRI) are used along with detailed dissections of unembalmed cadaveric material. Preliminary results on bonobo specimens show that bonobos have well-developed thumb muscles with similar basal thumb joint loading when compared to modern humans. However, in bonobos there is a functional coupling between the thumb and index finger as shown by their specific muscle configuration. Ultimately, our goal is a full documentation of our target species' thumb anatomy, the identification of interspecific variations, and investigating the biomechanical implications of the different anatomical configurations.

## Posters

### Ecology

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#### **Bioacoustics – A Non-Invasive Tool for Species Diagnosis in a Nocturnal Cryptic and Small-Bodied Primate Radiation, the Malagasy Mouse Lemurs (*Microcebus* spp.)?**

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Bioacoustics uses digital technology to record and analyze animal vocalizations to enhance our understanding of animal communication and to monitor animal health and biodiversity. Mouse lemurs represent the smallest-bodied extant primate radiation, are nocturnal and live in diverse Malagasy forests. This primate radiation comprises 24 genetically defined, phenotypically similar species. The conservation status of most species is barely known, but the often small geographical distribution makes them highly vulnerable to anthropogenically caused habitat disturbances, a major threat for lemurs' survival in Madagascar. The aim of this study was to explore, by a comparative and integrative bioacoustic, behavioural and genetic approach, whether the most frequently used mouse lemur calls bear species-specific signatures which would allow us, in the long run, to establish bioacoustic rapid assessment tools for surveying and monitoring species diversity in nature. We will present bioacoustic data from mouse lemurs, originating from 5 different study sites in northwestern and eastern Madagascar (Bombetok', Ampijoro', Mahatazana with dry deciduous forest and Lokobe National Park and Analamazaotra National Park with rain forest). The variation in vocalization and its use in signaling were determined by standardized bioacoustic methods using a social encounter paradigm ( $n = 12$  dyads/study site). Comparative data on agonistic calls between 6 genetically different cryptic species revealed a uniform acoustic contour, but species-specific statistical distinctiveness in acoustic structure. Acoustic divergence between species is predicted by genetic distance. The studied calls do not display habitat-specific differences, or play a major role in mate choice. Thus, our findings support an acoustic diversification caused by genetic drift. Furthermore, our approach reveals that mouse lemur vocalizations, often heard in nature, are species-specifically distinct and thus may be explored as a non-invasive tool for conservation.

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#### **Studies on Reproduction in Japanese Macaques – Ten Years of Collaboration between France and Japan**

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We report the outcomes of a 10-year Franco-Japanese collaborative research (2006 – present) on reproductive energetics and sexual signalling in the Japanese macaque (*Macaca fuscata*).

The main objectives of our research were to understand better the physiological and socio-environmental factors modulating female reproduction, but also to provide a complete overview of sexual signalling and mating strategies from both signallers (females) and perceivers (males) perspectives. We investigated the links between energetics (nutritional status, body composition) and reproductive outcomes in captive Japanese macaques. We showed that, even in captivity with relaxed energetic constraints, seasonal breeding entails relatively high energy costs, and that females with higher energy status could invest more in reproduction. We also investigated the information that males received from females that might enable them to discern periods with higher probabilities of conception and we developed a research programme on the extent to which Japanese macaques, a species lacking an obvious signal of reproductive status (i.e. no swelling), have evolved a system of multimodal sexual signalling. We provided information on the potential role of female behaviour, female skin colour, odours and vocalizations in male mating decisions. For instance, wild females advertised their pregnancy through changes in visual (face redness and luminance), behavioural, and, potentially, auditory signals, and males used these different sensory channels to adjust their mating behaviours and avoid wasting energy on non-reproductive copulations. This holistic project, using a multidisciplinary approach (behavioural observations, digital photography [measurements of female skin colour], hormonal [faecal ovarian steroids] and chemical data [components of urine and vaginal secretions]) suggests that Japanese macaques have evolved a system of multimodal sexual signalling as a trade-off between the costs and benefits of signalling and mating.

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### **Self-Medication Using Millipede Secretions in Red-Fronted Lemurs? Combining Anointment and Ingestion for Broad Anti-Parasitic Usage**

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Most of the millipedes (Diplopoda, arthropods) secrete a variety of chemicals which have sedative, repellent, irritant and toxic effects. Several species of birds and mammals have been observed to consume or use millipedes by rubbing them on their feathers or fur. This behaviour, being energetically costly, is thought to be associated with important benefits. It has been suggested that the millipedes' secretions may serve as protection against ectoparasites (including mosquitoes). In November 2016, in Kirindy Forest (Madagascar), the first heavy rain of the season elicited a massive reappearance of millipedes (*Sechelleptus* sp., Spirostreptidae). The next day we observed 6 red-fronted lemurs (*Eulemur rufifrons*) of both sexes, different age-classes and belonging to 2 different groups, anointing their perianal-genital areas and tail with bitten and salivated millipedes. Several individuals also ingested these millipedes entirely after a long chewing process. We discuss the different features of these behaviours, the nature and potential metabolic pathways of the released chemicals, and we suggest that millipede use may serve as an anti-parasitic activity, especially against digestive parasites present in their faeces, by combining anointment and ingestion behaviours.

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## Assessing the Distributions and Relative Abundances of Diurnal Primates (*Papio cynocephalus* and *Chlorocebus pygerythrus*) in Vwaza Marsh Wildlife Reserve, Malawi

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Very few studies address primate research and conservation in Malawi, although the as many as 7 primate species has been recorded in the country. Primates are absent from nearly all Malawi's national conservation action plans and policies. The Illegal Wildlife Trade Report of Malawi in 2015 comments on the absence of baseline data required by the Department of National Parks and Wildlife (DNPW) in order to create effective management and conservation strategies, and on the unreliability of previous wildlife datasets. Here, we aim to provide data and protocols that contribute to this dearth by assessing the distribution of diurnal primates in the Vwaza Marsh Wildlife Reserve (VMWR) and calculating their relative abundance. Pairs of researchers used distance sampling methods to record primate populations, covering 20 × 2 km line transects, with 2–3 repeats per transect over a 2 month study period. In order to assess vegetation structure throughout the study area, we applied the point centred quarter method of sampling, using points located every 40 m along transects. The two most commonly encountered primates, vervet monkeys (*Chlorocebus pygerythrus*) and yellow baboons (*Papio cynocephalus*), were found throughout VMWR. Yellow baboons were more likely to be found in open savannah, and vervet monkeys in denser thicket. Both species were common in forest dominated by *Brachystegia*, an important firewood resource for nearby communities. These findings directly contribute to primate conservation by enabling DNPW reserve managers to make informed decisions regarding biodiversity and conservation action plans. Establishing a protocol for measuring population densities is useful for the future monitoring of these species and promotes awareness of primate conservation policies in the area.

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## Nutritional and Phytochemical Composition of Young Leaves and Unripe Fruits Consumed by Proboscis Monkeys (*Nasalis larvatus*) in the Lower Kinabatangan Wildlife Sanctuary, Sabah, Malaysia

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Studying the nutritional content of the proboscis monkey diet is essential to provide a better understanding of the feeding strategy and nutritional ecology of this endangered colobine species. This research focuses on young leaves and unripe fruits consumed by free-ranging proboscis monkeys in the riverine forests of the Lower Kinabatangan Wildlife Sanctuary, in Sabah. Proboscis monkeys usually forage inland and return to the river to spend the night. While anti-predator strategies are the first explanation for this particular ranging pattern, the way the nutritional quality of leaves varies in riverine forests with the distance to the rivers should be investigated. During 8 months (2015–2016), we conducted morning and afternoon boat-based behavioural observa-



tions of unknown groups of proboscis monkeys present along the Kinabatangan River. Fifty-six tree and vine food species were recorded. Proximate analyses were carried out on 10 species that together accounted for more than 80% of proboscis monkey feeding occurrences at the riverside. For each sampled species, young leaves were collected from several individuals located on the riverbanks and for 5 of these species we also sampled young leaves from several individuals located further than 350 m inside the forest. Moreover, we sampled unripe fruits from *Nauclea orientalis* and *Ficus racemosa* at the riverside. Here, we aimed to test three main hypotheses: (1) that the chemical content of young leaves consumed by proboscis monkeys will follow the general trend of other colobine species – a high protein-fibre ratio; (2) that unripe fruits will contain more lipids than young leaves; and (3) that young leaves collected at the riverside will have a higher protein-fibre ratio and be richer in minerals than young leaves sampled further inland. Preliminary results show that unripe fruits contain  $6.42 \pm 1.82$  crude lipid % ( $n = 14$ ) while young leaves contain  $3.40 \pm 2.20$  ( $n = 57$ ). We also observed that crude ash % ( $6.62 \pm 1.43$ ,  $n = 72$ ) and NDF % ( $36.84 \pm 14.70$ ,  $n = 22$ ) follow the general trend of other colobines. This study will provide new insights on the feeding ecology of proboscis monkeys inhabiting secondary riverine forests. This information is crucial to understand better the feeding strategy of this endangered primate species and ensure its conservation.

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## Dietary Adjustment of Reintroduced Bornean Orangutans Relative to Their Rehabilitation History

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Orangutans are one of the most important species for the study of non-human animal culture. With their cultural repertoire and their close relatedness to humans, they contribute to our understanding of the evolution of our own culture. However, one of the main unanswered questions is the origin of innovations in orangutans. Since innovations lie at the root of every cultural behaviour, it is essential to understand in what context orangutans explore and innovate. Wild orangutans are known to depend strongly on social learning from their mothers to acquire their highly diverse diet. However, most reintroduced orangutans have been orphaned at a very young age. We used this natural experiment to evaluate how reintroduced orangutans with different backgrounds (especially time spent with humans and individual experience) adjust to their new environments, with an emphasis on their diet repertoire. From May 2016 until February 2017 we collected focal data on 10 Bornean orangutans, released by the BOS Foundation in Bukit Batikap, in Central Kalimantan: 6 mothers, 3 adolescent females and 1 unflanged male. For those 10 individuals, we have a total of 2,288 follow hours. We recorded the diet, food-related exploration and peering rates as well as time spent in association with other individuals. We are now comparing the number of species eaten (total and per day) between our focal animals with the data we have on the wild individuals in our study site in Tuanan. This is a preliminary study and the results and the discussion will be presented in the poster. However, based on former studies, we expect rehabilitated individuals to be more exploratory than wild ones and therefore to have a broader diet, and to rely more on low quality/low risk fall back foods. With this study, we hope to learn which factors determine the best release candidates and whether necessity has become the mother of invention in reintroduced orangutans.

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## **A Comparative Study on Fruit Preferences in *Macaca tonkeana*, *Macaca fascicularis* and *Sapajus* spp.**

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While foraging, primates need to discriminate between edible and non-edible food and to identify what food allows them to meet their nutritional needs. Many primate species show a broad dietary breadth and considerable diet flexibility while others are more specialized in their feeding choices. Because the environment in which a species has evolved shapes many aspects of animal life, including in captive conditions, we aimed at investigating how dietary variability may influence food preferences in three monkey species living in semi-free-ranging conditions at the Primate Centre of Strasbourg University. Preferences among 8 different types of fruits were investigated via a two-alternative choice test in 8 Tonkean macaques, 7 capuchin monkeys and 6 long-tailed macaques. Those species live in tropical forests but have different dietary tendencies that may affect their food preferences. The more frugivorous species should prefer higher soluble sugar content than the more generalist species. Therefore, we expect a higher impact of fruit sugar content in Tonkean macaques' preference than in long-tailed macaques and capuchins. The latter will also be influenced by the relative content of protein and fat concurrently to that of sugar in the same fruit types. In comparison to the Tonkean macaques, these species may thus have a stronger preference for more nutritionally complete fruit since they include higher percentages of animal matter and seeds in their diet. Preliminary analyses of results from the Tonkean macaques show a strong positive correlation between preference of fruit type and its total sugar content. For the other two species, results are being analyzed and will be discussed according to our comparative predictions. This study provides insights into the ecological and evolutionary adaptations of primates' food choice.

## **Poster Communication**

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## **Ontogeny of Female-Specific Great Calls in Juvenile and Adolescent Gibbon Males *Nomascus gabriellae***

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Vocalizations in gibbons are very interesting to analyse, as they contain complex species- and sex-specific patterns. In the southern yellow-cheeked gibbon (*Nomascus gabriellae*), adult males produce a sound structure that consists of a "staccato" note and a "multi-modulation" phrase (coda phrase). Staccato notes are very subtle and produced in short, irregular series. Multi-mod-

ulation phrases belong to dominant acoustic structures. A female-specific vocalization, the “great call,” has typically 5–13 notes that further split into “oo” notes, “bark” notes and a “twitter” part. Despite this, the ontogeny of gibbon song has received little attention and how the males and females develop their sex-specific duet roles remain unclear. Recently, it has been documented that immature gibbon males can produce great calls. However, regular production of great calls was mentioned without more detailed investigation. Our research was conducted in two Czech zoological parks (Olomouc and Jihlava) from March to May 2014 and from October to December 2014. Spontaneous vocalizations were recorded 2 to 6 times per month from 5:00 to 12:30 a.m. within a distance of 2 to 15 metres from the gibbons. All data were analysed with the aid of the SAS System version 9.4 (SAS Institute Inc.). General Linear Mixed Models (GLMM – PROC GLIMMIX and PROC MIXED) were used for the analysis. We recorded songs using the M-Audio Micro Track II recorder with a Rode NTG-2 semi-directional microphone with 16-bit resolution and a 96 kHz sampling rate. Sampling frequency was reduced from 96 kHz to 12 kHz for further analyses. Acoustic analysis was performed using Avisoft SASLab pro version 5.2 (Avisoft Bioacoustics, Berlin, Germany). Spectrograms were generated with the following settings (FFT length = 1,024, frequency resolution = 12 Hz, temporal resolution = 21.3 ms, overlap = 75%, window type = Hamming). To characterize great calls we measured the onset frequency (beginning of the first syllable), the offset frequency (at the beginning of the last syllable preceding the twitter) and noted the presence of the twitter part. Here, we document regular production and ontogenetic changes of the female-specific great call in 4 immature male (2 juveniles – ca. 3 years old; and 2 adolescents – ca. 5 years old) southern yellow-cheeked gibbons over a period of 9 months. None of the males produced fully developed adult-like great calls. Great calls of sons were shorter than those of their mothers. Immature males (adolescents and juveniles) had a higher first syllable, a lower last syllable ( $F_{(2, 181)} = 23.24, p < 0.0001$ ) and a lower number of syllables than adult females ( $F_{(2, 181)} = 23.24, p < 0.0001$ ). Regular production of the twitter part of the great call likely appears around 4 years of age as it was observed in adolescent but not in juvenile males ( $F_{(2, 181)} = 23.24, p < 0.0001$ ). Our results indicate an interesting degree of flexibility and suggest a new significance of the sex-specific vocalization in *Nomascus* gibbons.

## Poster

### Non-Invasive Health Monitoring

#### Faeces Matter! Non-Invasive Monitoring of Stress and Health in Wild Primates

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As infectious diseases are putting more pressure on declining animal populations and zoonotic outbreaks are increasing in frequency and severity, stress and health monitoring in wildlife seems crucial for both conservation plans and human health management. However, ethical and practical difficulties for health monitoring of wild animals are more the rule than the exception. Here, we present a few techniques specifically developed or used within the Research Group “Sociality and Health in Primates” funded by the “Deutsche Forschungsgemeinschaft” (DFG). We focused on non-invasive techniques requiring little to no cooperation from the animals, using saliva, urine or faeces to measure short-term and long-term stress levels, inflammation reaction, immune system activation, nutritional status and parasites and pathogens in 6 projects with dif-

ferent primate species. We show that non-invasive monitoring of stress and health in wildlife can be easily conducted in field conditions, with regular collection of products usually considered as waste and without stress or disturbance of the animals' behaviour and physiology. We believe that these methods can allow better monitoring of endangered animal populations and zoonotic outbreaks with an enhanced understanding of the sociality-stress-health relationship in group living animals.

## Poster

## Nutrition

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### **Diet Transition Assessment in Laboratory Long-Tailed Macaques (*Macaca fascicularis*)**

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Laboratory primates' diets have a stable composition in order to fulfill nutritional needs and avoid experimental bias. A drastic change in alimentation might induce digestion issues due to unbalanced intestinal flora. Such changes can occur in a primate's life when it is transferred from a breeding site to experimental facilities. Therefore a period of acclimatization with a transition diet is required for the animal's health and relevant research. In this study, we tested this kind of transition with a new diet for Old World monkeys that fits the needs of long-tailed macaques, which is the most common species used for scientific purposes in Europe. The new diet was tested in 2 groups of macaques, a reproductive group of 10 males and 9 females, and a group of 11 young males. All of the individuals were weighed and their body score assessed before and after the study. Animals were group-housed in large indoor/outdoor rooms with ad libitum access to food and water. A defined quantity of pellets was distributed once a day at one feeding point. To evaluate food consumption, feeders were emptied before distribution and the remaining food weighed for both diets. The protocol began with a 1 week-period of transition with mixed diets in equal parts, then the animals received a single diet as a daily ration. We monitored potential short-term changes (feeding behaviours) in the reproductive group composed of subjects of different ages and weights. The young male group was followed for a longer period to evaluate the impact of the new diet on weight intake. The data collected revealed a difference in appetite for the new diet that should be assessed with regards to the breeding history of the animals, flavouring and neophobic behaviour. Zootechnical parameters demonstrated that the animals' condition and weight remained stable in the short-term while they seemed to progress normally in the long term.

## Poster

### Reproduction and Social Factors

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#### Colour Change and the Onset of Ovarian Cycle in *Nomascus* Females

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Gibbons of the genus *Nomascus* exhibit strong sexual dichromatism. Fur colour in sub-adult females typically changes with the onset of puberty and is usually associated with the start of the ovarian cycle. There are also several examples regarding the probable onset of a female's menarche before the change of hair colour from black to beige, especially in captivity. These behavioural changes result from specific conditions within the habitat or inside the social group. Based on this information, we presupposed that social factors may affect the coat colour and that the onset of the ovarian cycle (OC) would occur before the colour change. Four sub-adult females, *Nomascus leucogenys* (3) and *N. gabriellae* (1), were used for hormone analysis of progesterone and oestrogen metabolites to determine the start of the OC. Collection of faecal samples was carried out in four zoos (Liberec, Usti, Asson, Bratislava); the average number of samples per cycle was  $4.7 \pm 0.95$ . We used the non-invasive (ELISA) method for metabolite analysis. Results showed that individuals started to reach sexual maturity between the ages of 4.6–5.8 years old. Zoo facilities (presence of mother or other gibbons), composition of the gibbon group (family, pair, offspring), and a record of colour change of individual females were recorded. All of this information was used to evaluate the possible factors influencing hair colour change. This preliminary study showed that OC onset is not correlated with the fur colour change, but the variation in timing of the final colour change, based on the zoo data, may have been connected with the presence or absence of the mother. This pilot research indicates more profound and possibly multi-factorial connections, leading to the conclusion that we should have assessed a wider range of females between the ages of 4 and 7 years old. Further long-term studies including all social factors are needed to better understand female dominance in crested gibbons.

## Posters

### Welfare

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#### From a Laboratory to a Rescue Centre: Preliminary Study for the Rehabilitation of a Colony of Long-Tailed Macaques (*Macaca fascicularis*)

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*Macaca fascicularis* is one of the most common primate species used in laboratories. After their participation in laboratory experiments, some animals are rehabilitated in facilities such as rescue centres. The process of rehabilitation varies depending on many factors such as the type

of experiment conducted on the individual, the living environment and the type of care provided. The aim of our project was to provide the animals with an appropriate species-typical environment, with the intention of reducing problematic behaviours and avoiding new stereotypic behaviours and finally to reunite the colony. Our long term objective is the development of a standardized protocol for the rehabilitation of non-human primates previously housed in laboratories. The study group is a colony of 16 *M. fascicularis* (9 males, 7 females), housed under laboratory conditions since 1999 and transferred to the rescue centre in July 2016. On arrival, some of the individuals displayed stereotyped behaviours and symptoms of alopecia. Daily observations of the colony and focal sample observations of the individuals displaying stereotyped behaviours were conducted before implementation of the rehabilitation protocol. Males and females were then gradually integrated into a single colony. They were given access to an outside enclosure furnished with wooden structures and other enrichments. An enrichment programme was also introduced, including manipulatory/foraging enrichments and PME: a specialist psycho-social enrichment for non-human primates. The preliminary results of this study show that after 3 months of implementation of the rehabilitation programme we could observe a progressive decrease in alopecia and stereotypic behaviours (i.e. pacing from 58% of the time to 0%) and we conclude that providing a species-adapted 'free-range' enclosure supplemented with a variety of fresh food and specialized enrichments, significantly improved the welfare conditions of the rehabilitated colony.

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### Local Community Perceptions and Knowledge of Appropriate Living Conditions for Captive Primates and Implications for the Welfare of Pet Monkeys on Peninsula de Paria, Venezuela

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Despite conservation initiatives, and the fact that capturing and/or selling primates is illegal in Venezuela, the number of primates kept as pets is increasing. The Venezuelan north coast is one of the major regions of origin of primates taken illegally as pets in the country. Gaps already identified in local knowledge and perceptions of wild primates as pets present a challenge in stopping the illegal pet trade and improving pet-primate welfare; showing a need to evaluate the pet trade's scope on all levels. To address this, we conducted a study of the local perceptions and knowledge of primate pets and the impact of their captive environment on the welfare of the pet primates on Peninsula de Paria, Sucre state, Venezuela. We collected data on (a) species identification, wild capture origin, age, diet and husbandry and (b) respondents' demographics and their perceptions and knowledge of primates as pets through semi-structured interviews with local families – potential pet owners ( $n = 30$ ). To raise awareness about primates and their ecology, we designed age and culturally appropriate educational materials, and distributed them to the respondents. We found that wedge-capped capuchins (*Cebus olivaceus*) are the most common pet primate, followed by howler monkeys (*Alouatta arctoidea*). Most observed were  $\leq 5$  years old, and often considered as a family member. Despite high scores for species recognition, respondents' knowledge about primate ecology was poor. Consequently, animals were kept in inadequate conditions and received an inappropriate diet – a major cause of primate health issues. Along with better law enforcement; long-term education campaigns are needed to raise awareness about the importance of wild primate species, and to educate current primate pet owners on ways to improve their welfare. To scale up the effectiveness of the approaches mentioned, we note the need to connect local initiatives into a regional and national conservation and welfare network.